PhytoKeys 152: 1–14 (2020)
doi: 10.3897/phytokeys.152.53512
http://phytokeys.pensoft.net

RESEARCH ARTICLE

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PhytoKeys
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A new species of *Bredia* (Sonerileae, Melastomataceae) from Sichuan, China

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Academic editor: Ricardo Kriebel | Received 23 April 2020 | Accepted 18 May 2020 | Published 3 July 2020

Citation: Dai J-H, Zhou Q-J, Zhou R-C, Liu Y (2020) A new species of *Bredia* (Sonerileae, Melastomataceae) from Sichuan, China. PhytoKeys 152: 1–14. https://doi.org/10.3897/phytokeys.152.53512

Abstract

Bredia hispida (Sonerileae, Melastomataceae), a species occurring in southeastern Sichuan, China, is newly described based on morphological and molecular data. The generic placement of *B. hispida* is well supported by phylogenetic analysis and morphological characters, including basally cordate, hairy leaf blade, cymose inflorescence, basally gibbous anthers and enlarged ovary crown enclosing an inverted frustum-shaped depression. Both molecular and morphological divergence showed that *B. hispida* is well separated from its close relatives, justifying its recognition as a distinct species. The new species resembles *B. repens*, *B. changii* and *B. guidongensis* in the prostrate habit and isomorphic stamens but differs markedly in the unequal opposed leaves, the 2–4 mm long, stout bristles on the adaxial surface of leaf blade and acuminate leaf apex. *Bredia hispida* co-occurs with *B. esquirolii* in the wild. No morphologically putative hybrids between them were observed despite their overlap in flowering season. The isolating mechanism remains unclear, pending further investigation.

Keywords

Bredia, Melastomataceae, phylogeny, taxonomy

Introduction

Bredia Blume was originally established based on *B. hirsuta* Blume, a species endemic to Taiwan and the Ryukyu islands (Blume 1849). Circumscription of this genus had long been controversial. The dispute mainly concerned whether to include *Tashiroea* Matsum. ex T. Itô & Matsum. and certain species of *Phyllagathis* Blume in *Bredia* (Diels

1924, 1932; Merrill and Chun 1940; Li 1944; Chen 1979, 1984; Hansen 1992; Chen and Renner 2007). By combining molecular phylogenetic and morphological data, recent studies have provided strong evidence for a new generic limit of *Bredia* (Zhou et al. 2019a, 2019b, 2019c). *Bredia* was redefined as excluding *Tashiroea* while incorporating seven species previously treated in *Phyllagathis* (Zhou et al. 2019b). Together with two recently published species, *Bredia* as currently circumscribed includes 23 species distributed from central and southern mainland China, Taiwan, to the Ryukyu islands and northern Vietnam (Zhou et al. 2019b; Wen et al. 2019; He et al. in press). Species of *Bredia* are characterized by the leaf blade papery, usually hairy, inflorescences cymose, umbellate, or a cymose panicle, anther basally gibbose or tuberculate, and ovary crown persistent and enlarged enclosing an inverted frustum-shaped depression.

During a survey of specimens in Chinese herbaria for a project on species delimitation of *Bredia*, several collections from Xuyong County, southeastern Sichuan Province, caught our attention. These collections (e.g. Fig. 1A–C) were identified as *Phyllagathis deltoidea* C. Chen (Fig. 1D–F). Upon closer examination, however, the plants from Xuyong are morphologically quite different from *P. deltoidea* in having basally cordate (vs. cuneate) lamina adaxially hispid with stout long bristles (vs. puberulous and sparsely setose) and linear-lanceolate calyx lobes (vs. broadly triangular lobes) (Fig. 1). In addition, *P. deltoidea* is only recorded from its type locality in Ningming County, southwestern Guangxi, which is about 800 kilometers away from Xuyong County, southeastern Sichuan. Both morphology and distribution suggest that the current identification is erroneous.

In September 2019, we made a field expedition to Xuyong County and collected flowering and fruiting specimens of the plant in question (Figs 2, 3). This plant possesses all the synapomorphies of *Bredia* aforementioned. It most closely resembles *B. changii* W. Y. Zhao, X. H. Zhan & W. B. Liao, *B. guidongensis* (K. M. Liu & J. Tian) R. Zhou & Ying Liu and *B. repens* R. Zhou, Q. J. Zhou & Ying Liu in habit and isomorphic stamens (Fig. 4), but differs markedly from the latter species in leaf morphology (Fig. 2). Judging from morphological aspects, this plant may represent an undescribed species in *Bredia*.

To test the generic affiliation of the unknown plant and its closest relative in the genus, we performed phylogenetic analyses based on DNA sequence data of nuclear ribosomal internal transcribed spacer (nrITS), sampling all species so far recorded in *Bredia*. We also calculated pairwise genetic distances among this plant and 23 species of *Bredia* to evaluate its distinctness. The results confirmed our suspicion that this plant represented a species new to science, which we described as *B. hispida* below.

Materials and methods

To test the generic affiliation of *B. hispida* and its position in the genus, we selected ingroup taxa based on previous studies (Zhou et al. 2019a, 2019b, 2019c). The final nrITS dataset contained 35 accessions representing *Blastus* Lour., *Dissochaeta* Blume,

Figure 1. Herbarium specimen of *Bredia hispida* (**A–C**) and *Phyllagathis deltoidea* (**D–F**). **A–C** W. B. Ju and H. N. Deng, HGX12702 (CDBI) collected from Shui-wei town, Xuyong County, Sichuan, China, showing the stout long bristles on adaxial surface of the leaf blade and linear-lanceolate calyx lobes, images from National Plant Specimen Resource Center **D–F** H. H. Su 68119 (IBK, IBSC) collected from Aidian, Ningming County, Guangxi, China, holotype (IBSC) (**D, F**) and isotype (IBK) (**E**) of *Phyllagathis deltoidea*.

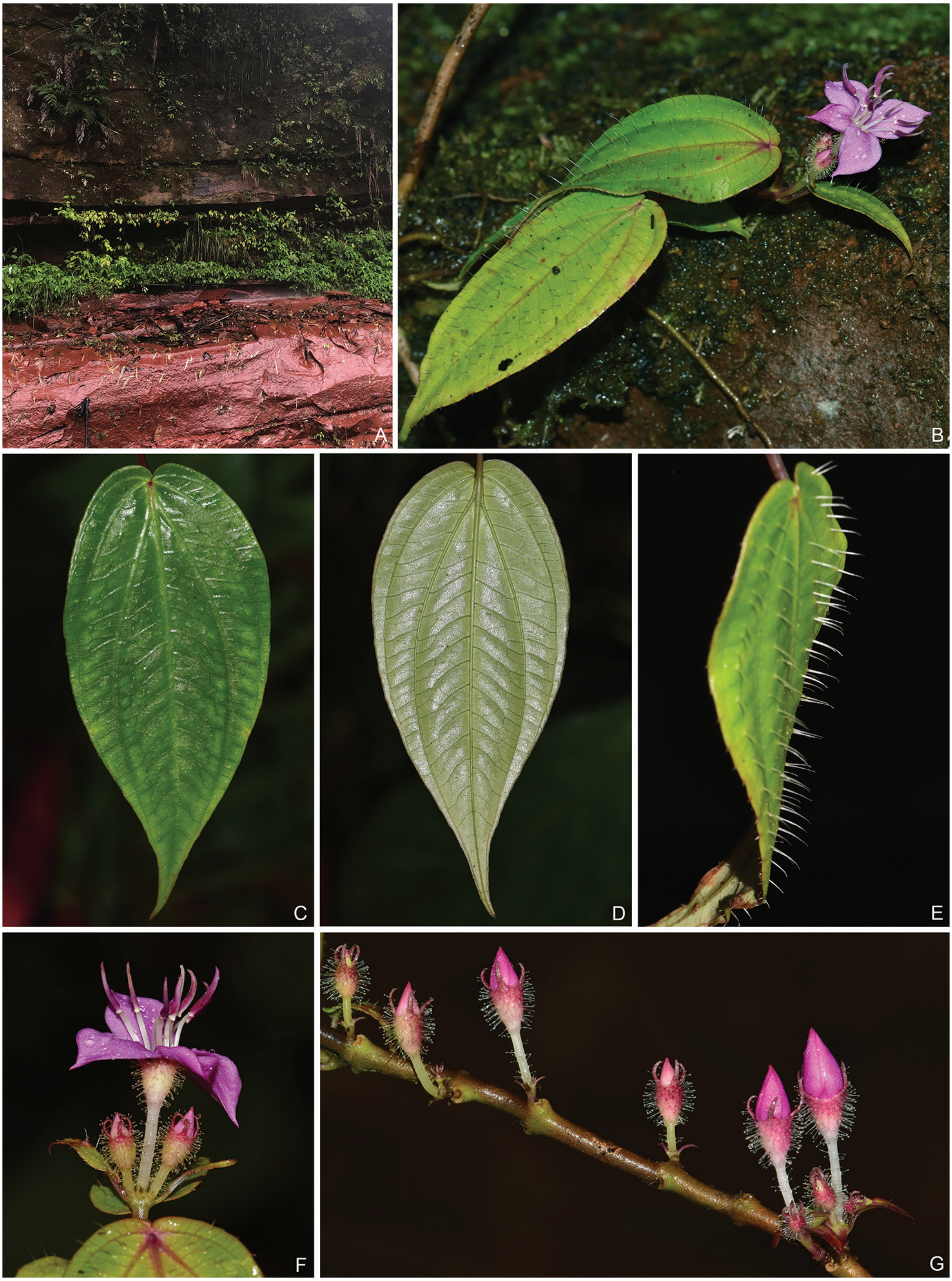

Figure 2. *Bredia hispida*. **A** Habitat **B** a flowering branch, showing the prostrate habit **C** adaxial leaf surface **D** abaxial leaf surface **E** lateral view of leaf, showing the stout long bristles **F** terminal inflorescence **G** axillary inflorescences on old branchlets. All from Y. Liu 764 (A, PE, SYS).

Figure 3. Floral details and young fruit of *Bredia hispida.* **A** Side view of a flower **B** top view of a flower **C** longitudinal section of a flower showing isomorphic stamens and ovary crown **D** top view of a young fruit **E** side view of a young fruit showing enlarged ovary crown exserted from hypanthium. Scale bar: 5 mm (**C**). All from Y. Liu 764 (A, PE, SYS).

Fordiophyton Stapf, *Tashiroea*, *Phyllagathis*, *Scorpiothyrsus* H. L. Li, *Blakea* P. Browne, and 23 species so far recorded in *Bredia*, with *Blakea* (Blakeeae) chosen as an outgroup according to Goldenberg et al. (2012). The sequences of *B. hispida*, *B. violacea* H. L. Li and *B. reniformis* C. M. He, Y. H. Tong & S. J. Zeng were newly sequenced, while the rest were downloaded from GenBank. The source of the materials and GenBank accession numbers are given in Supplementary material 1.

Figure 4. Three prostrate species of *Bredia*. **A** *B. guidongensis* from Y. Liu 472 (SYS) **B** *B. changii* from Y. Liu 548 (SYS) **C** *B. repens* Y. Liu 558 (A, PE, SYS).

Total DNA was extracted from fresh leaves using the modified CTAB procedure (Doyle and Doyle 1987). The nrITS region of *B. hispida*, *B. violacea* and *B. reniformis* were amplified and sequenced using universal primers ITS4 and ITS5 (White et al. 1990), following the procedure described in Zou et al. (2017).

Sequences were aligned using SeqMan v.7.1.0 (DNASTAR Inc., Madison, WI). The Akaike information criterion in Modeltest version 3.7 (Posada and Crandall 1998) was used to select the best-fitting nucleotide substitution model (GTR+G) prior to phylogenetic analyses. Bayesian inference (BI), maximum likelihood (ML) and maximum parsimony (MP) analyses were performed using MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001), RAxML version 8.2.10 (Stamatakis 2014) and PAUP version 4a165 (Swofford 2002) respectively. For BI analysis, two independent Markov chain Monte Carlo analyses (MCMC) were performed with four simultaneous chains of 2,000,000 generations sampling one tree every 100 generations. The first 25% of trees were discarded as burn-in and the remaining were used to construct a majority-rule consensus tree with Bayesian posterior probabilities (PP). We verified that the average deviation of split frequencies had reached a value below 0.01 at the end of MCMC analyses. We also assessed the effective sample sizes (ESS) for all parameters and statistics using Tracer version 1.7.1 (Rambaut et al. 2018). ML analyses were performed under GTR+G model as recommended by the author. Node support was estimated with 1,000 bootstrap replicates using a fast bootstrapping algorithm (Stamatakis et al. 2008). For MP analyses, a heuristic search strategy was conducted of 1000 random addition replicates, with the tree-bisection-reconnection (TBR) branch swapping algorithm and MultTrees on. Maxtree was set to 500. Node support was evaluated by 1000 bootstrap replicates of 1000 random additions. Pairwise genetic distances among *B. hispida* and species of *Bredia* were calculated using the Kimura 2-parameter method (Kimura 1980).

Results

The aligned sequence matrix contained 665 characters. Statistics of sequences sampled were summarized in Supplementary material 2. The tree resulting from ML analysis is shown in Fig. 5, with PP, ML bootstrap support values (BSML), and MP bootstrap support values (BSMP) labeled at nodes. *Bredia hispida* was nested within the well supported *Bredia* clade (PP = 1.0, BSML = 100%, BSMP = 96%), forming a subclade with *B. repens*, *B. tuberculata* (Guillaumin) Diels and *B. yunnanensis* (H. Lév.) Diels (PP = 1.0, BSML = 87%, BSMP = 81%). Pairwise genetic distances among *B. hispida* and 23 species of *Bredia* are provided in Supplementary material 3.

Discussion

Phylogenetic position and specific status of *B. hispida*

The placement of *B. hispida* in *Bredia* is supported by phylogenetic and morphological data. Our phylogenetic analyses with complete taxon sampling of *Bredia* confirmed that *B. hispida* is a member of this clade. Morphologically, its basally cordate, hairy leaf blade, cymose inflorescence, two whorls of eight isomorphic stamens, basally slightly gibbous anthers, decurrent connectives, and enlarged ovary crown during the fruiting stage all fit well within *Bredia*.

Bredia hispida is phylogenetically most closely related to *B. repens*, *B. tuberculata* and *B. yunnanensis*. It is a dwarf subshrub up to 15 cm tall with its middle and lower

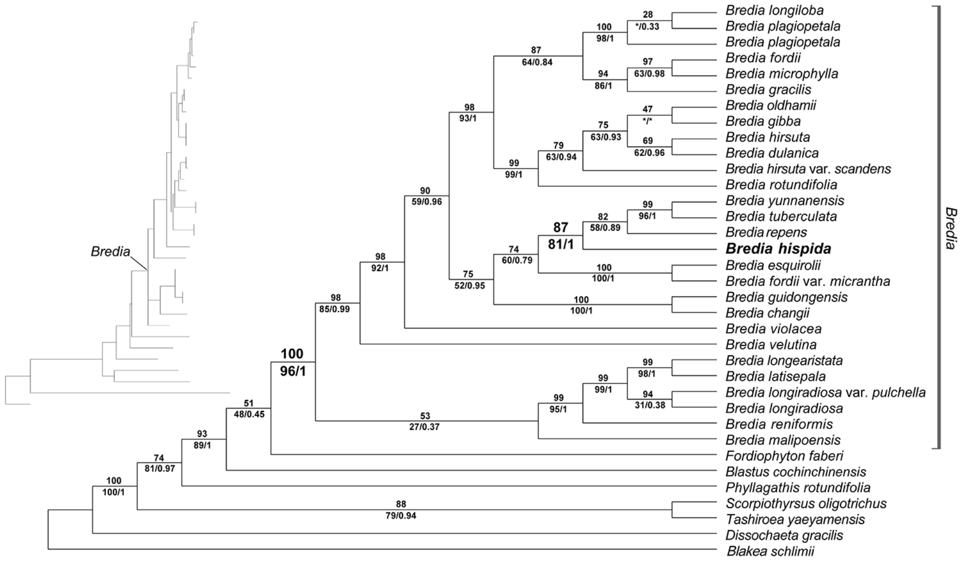

Figure 5. Phylogenetic position of *Bredia hispida*. Maximum likelihood (ML) phylogenetic tree based on nrITS sequence data. Numbers above branches are bootstrap values obtained from maximum likelihood analyses, and those below branches are Bayesian posterior probabilities (right) and bootstrap values (left) resulting from maximum parsimony analyses. The new species is noted in bold. Asterisk denotes a branch collapsed in Bayesian inference or maximum parsimony analyses.

stem prostrate, which makes it easily distinguished from most species of *Bredia*, including *B. tuberculata* and *B. yunnanensis*. It closely resembles *B. guidongensis* (Fig. 4A), *B. changii* (Fig. 4B) and *B. repens* (Fig. 4C) in the prostrate habit and isomorphic stamens, but differs in leaf morphology: opposed leaves unequal, leaf blade larger (1.5–9.9 × 0.8–4 cm), stiffly papery, ovate to ovate elliptic and apically acuminate (Fig. 2B–E). Moreover, *B. hispida* is unique in the genus in its leaf blade adaxially hispid with 2–4 mm long, stout bristles (Fig. 2E), a character previously never recorded in *Bredia*. Pairwise genetic distances between *B. hispida* and remaining species of the genus range from 0.011 to 0.066, which are comparable to the distances of most species pairs in *Bredia* (0.005–0.077). *Bredia hispida* is therefore well diverged from other species of *Bredia* from a molecular perspective. Both molecular and morphological evidence justify the recognition of *B. hispida* as a distinct species.

Co-occurrence of *B. hispida* and *B. esquirolii*

Bredia hispida is currently only known from Xuyong County, Sichuan Province. It co-occurs with *B. esquirolii* (H. Lév.) Lauener, a species widely distributed in Guizhou, Chongqing and Sichuan. *Bredia hispida* grows on shady red sandstone cliff of seasonal waterfall whereas *B. esquirolii* is found in bushes, under forests and also on shady cliff (but a little further away from the dripping water). Several cases of sympatry have been observed elsewhere in the genus, viz. *B. dulanica* C. L. Yeh, S. W. Chung & T. C. Hsu and *B. oldhamii* Hook. f. in Taiwan, *B. repens* and *B. latisepala* (C. Chen) R. Zhou & Ying Liu in Hunan and *B. esquirolii* and *B. tuberculata* in Sichuan. In the first two cases, the co-occurring species have non-overlapping flowering seasons and thus interspecific reproductive isolation is easily maintained; in the third case, the flowering periods overlapped, and some putative hybrid individuals were found (unpublished data). During our visit in September 2019, both *B. hispida* and *B. esquirolii* were flowering. But no morphologically putative hybrids were observed. Pre-zygotic isolation via different pollinators is not a plausible explanation as flowers of the two species are of similar size (ca. 2 cm in diameter) and both can be visited by medium to small size bees. According to previous analyses (Zhou et al. 2019c), the crown age of the branch comprising close relatives of *B. hispida*, viz. *B. esquirolii*, *B. repens*, *B. tuberculata* and *B. yunnanensis*, was only 0.66–2.61 Mya. We suspect that other intrinsic postzygotic barriers may not have enough time to fully develop among such recently diverged species. The isolation mechanism between the sympatric *B. hispida* and *B. esquirolii* remains unclear, pending further study.

Taxonomic treatment

Bredia hispida **J.H. Dai & Ying Liu, sp. nov.**

urn:lsid:ipni.org:names:77209989-1
Figures 2, 3, 6

Type. China. Sichuan: Xuyong County, Shui-wei town, Guang-mu village, 1338 m, on steep rock cliff of a small waterfall, 1 Sept 2019, Ying Liu 764 (holotype: PE; isotype: A, SYS).

Diagnosis. Resembles *B. changii*, *B. repens* and *B. guidongensis* in the prostrate habit and isomorphic stamens but differs from these species in its unequal leaves (vs. equal), stiffly papery leaf blade (vs. papery) hispid with 2–4 mm long, spreading stout bristles (vs. pubescent or villous with trichomes ≤ 1 mm) and acuminate apex (vs. obtuse or acute).

Description. Subshrubs, up to 15 cm tall. Stems cylindrical, inconspicuously pubescent with very short, uniseriate appressed trichomes, prostrate at middle and lower parts, branched, with adventitious roots. Opposed leaves often unequal; petiole 0.6–5 cm long, inconspicuously pubescent; leaf blade ovate to ovate elliptic, larger blades 4–9.9 × 1.6–4 cm, smaller blades 1.1–5× 0.7–2.5 cm, stiffly papery, abaxial surface pale green, inconspicuously pubescent, adaxial surface green to yellowish green, inconspicuously pubescent, hispid with spreading stout white bristles (2–4 mm long) between veins, lateral veins 2 or 3 pairs, base cordate, margin inconspicuously serrulate, apex acuminate. Inflorescences terminal or axillary, sometimes on old branchlets; 2–3-flowered cyme or solitary. Peduncle 2–10 cm long, pubescent with uniseriate appressed trichomes. Flowers bisexual, radial but androecium slightly bilateral, 4-merous, rarely 5-merous.

Figure 6. Holotype of *Bredia hispida*, Y. Liu 764 (PE). Scale bar: 5 cm.

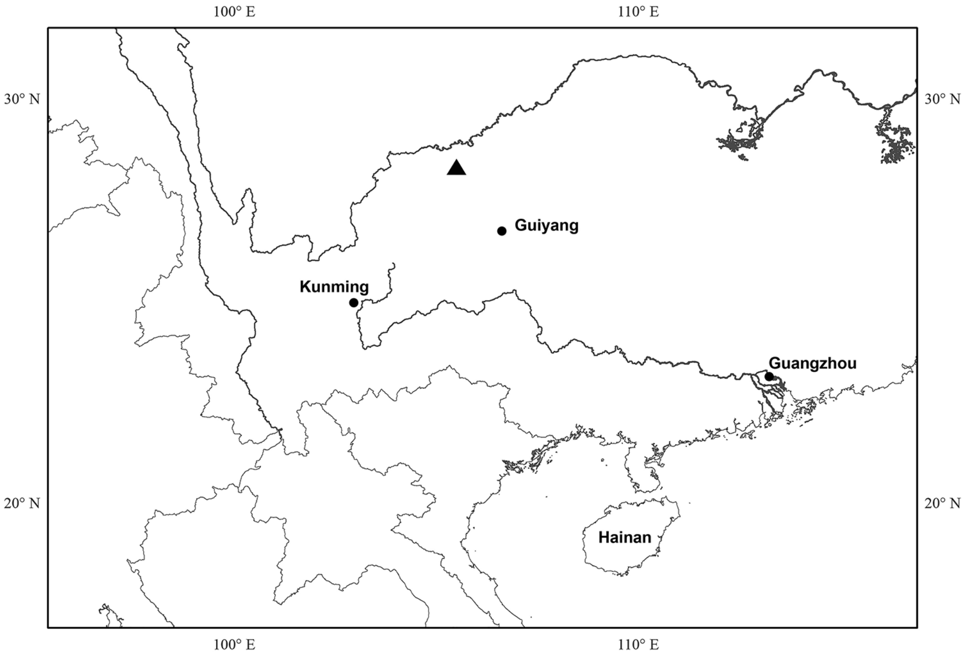

Figure 7. Distribution of *Bredia hispida* (triangle).

Pedicels and calyces pubescent with uniseriate appressed trichomes and multiseriate spreading glandular trichomes. Pedicels 7–16 mm long. Hypanthium cup-shaped, ca. 4 × 4 mm, pubescent with spreading glandular trichomes. Calyx lobes 4, linear-lanceolate, ca. 3–4 mm long. Petals 4, purplish pink, ovate, 7 × 5 mm, slightly oblique, apex acute. Stamens 8, isomorphic, subequal in length, 8–10 mm long. Anthers purplish, bilocular, lanceolate, ca. 4–5.5 mm long, base slightly gibbous, connective decurrent, forming a tuberculate appendage dorsally. Ovary half inferior, locules 4, placentation axillary, ovary apex with a membranous crown, crown margin ciliate with glandular trichomes. Style ca. 11 mm long, puberulous in the lower part. Young fruit cup-shaped, apex crowned, crown exserted from hypanthium. Seeds numerous, premature.

Phenology. Flowering July–September, young fruits in September.

Etymology. The specific epithet is based on the spreading stout bristles on the leaf blade of this species.

Distribution. *Bredia hispida* is currently known from Xuyong County, southeastern Sichuan, China (Fig. 7). It occurs on damp steep red sandstone cliff, often below a seasonal waterfall, at 1000–1400 m.

Additional specimen examined. China. Sichuan: Xuyong County, Shui-wei town, Guan-dou village, 15 Sept 2013, W. B. Ju and H. N. Deng, HGX13524 (CDBI); Xuyong County, Shui-wei town, Guang-mu village, 27 Aug 2013, W. B. Ju and H. N. Deng, HGX12702 (CDBI); Xuyong County, Long-feng town, Ling-guan-ti power station, 4 Aug 2012, X. F. Gao, Y. D. Gao and W. B. Ju, HGX10961 (CDBI).

Acknowledgements

We thank Herbarium of Chengdu Institute of Biology (CDBI) for their kind assistance during herbarium survey. We are grateful to Dr. David E. Boufford and the anonymous reviewer for their valuable comments on the manuscript. This work was supported by the National Natural Science Foundation of China (31770214), Science and Technology Program of Sichuan Province (2018JY0487) and Science and Technology Project of Yuexiu District, Guangzhou City (2018-GX-001).

References

Blume CL (1849) Melastomataceae. Museum Botanicum Lugduno-Batavum 1: 1–25.

Chen C (1979) Melastomataceae. In: Wu ZY (Ed.) Flora Yunnanica, vol. 2. Science Press, Beijing, 77–137.

Chen C (1984) Melastomataceae. Flora Reipublicae Popularis Sinicae. Science Press, Beijing, 53: 135–293.

Chen C, Renner SS (2007) Melastomataceae. In: Wu ZY, Raven PH, Hong DY (Eds) Flora of China, vol. 13. Science Press, Beijing, Missouri Botanical Garden Press, St. Louis, 360–399.

Diels L (1924) Miscellanea sinensia I. Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9(83): 197–199. https://doi.org/10.2307/3994336

Diels L (1932) Beiträge zur Kenntnis der Melastomataceen Ostasiens. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 65: 97–119.

Doyle JJ, Doyle JL (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemical Bulletin 19: 11–15.

Goldenberg R, de Fraga CN, Fontana AP, Nicolas AN, Michelangeli FA (2012) Taxonomy and phylogeny of *Merianthera* (Melastomataceae). Taxon 61(5): 1040–1056. https://doi.org/10.1002/tax.615010

Hansen C (1992) The genus *Phyllagathis* (Melastomataceae): Characteristics; delimitation; the species in Indo-China and China. Bulletin du Museum National d'Histoire Naturelle. Section B, Adansonia, Botanique. Phytochimie 14: 355–428.

He CM, Zeng SJ, Li SW, Tong YH (in press) *Bredia reniformis* (Melastomataceae), a new species from Guangxi, China. Nordic Journal of Botany.

Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics (Oxford, England) 17(8): 754–755. https://doi.org/10.1093/bioinformatics/17.8.754

Kimura M (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16(2): 111–120. https://doi.org/10.1007/BF01731581

Li HL (1944) Studies in the Melastomataceae of China. Journal of the Arnold Arboretum 25: 1–42. https://www.jstor.org/stable/43781108

Merrill ED, Chun WY (1940) Additions to our knowledge of the Hainan flora. Sunyatsenia 5: 45–200.

Posada D, Crandall KA (1998) Modeltest: Testing the model of DNA substitution. Bioinformatics (Oxford, England) 14(9): 817–818. https://doi.org/10.1093/bioinformatics/14.9.817

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67(5): 901–904.

Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics (Oxford, England) 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML web servers. Systematic Biology 57(5): 758–771. https://doi.org/10.1080/10635150802429642

Swofford DL (2002) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Wen ZY, Zeng SJ, Fan W, Zhang GQ, Peng DH (2019) *Bredia malipoensis* (Melastomataceae), a new species from Yunnan, China. Phytotaxa 425(3): 127–136. https://doi.org/10.11646/phytotaxa.425.3.2

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis M, Gelfand D, Sninsky J, White TJ (Eds) PCR Protocols: A guide to methods and applications. Academic Press, San Diego, 315–332. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Zhou QJ, Lin CW, Dai JH, Zhou RC, Liu Y (2019a) Exploring the generic delimitation of *Phyllagathis* and *Bredia* (Melastomataceae): A combined nuclear and chloroplast DNA analysis. Journal of Systematics and Evolution 57(3): 256–267. https://doi.org/10.1111/jse.12451

Zhou QJ, Dai JH, Lin CW, Denda T, Zhou RC, Liu Y (2019b) Recircumscription of *Bredia* and resurrection of *Tashiroea* (Sonerileae, Melastomataceae) with description of a new species *T. villosa*. PhytoKeys 127: 121–150. https://doi.org/10.3897/phytokeys.127.36608

Zhou QJ, Lin CW, Ng WL, Dai JH, Denda T, Zhou RC, Liu Y (2019c) Analyses of plastome sequences improve phylogenetic resolution and provide new insight into the evolutionary history of Asian Sonerileae/Dissochaeteae. Frontiers of Plant Science 10: 1477. https://doi.org/10.3389/fpls.2019.01477

Zou PS, Ng WL, Wu W, Dai SP, Ning ZL, Wang SQ, Liu Y, Fan Q, Zhou RC (2017) Similar morphologies but different origins: Hybrid status of two more semi-creeping taxa of *Melastoma*. Frontiers of Plant Science 8: 673. https://doi.org/10.3389/fpls.2017.00673

Supplementary material 1

Table S1. Source of materials studied and GenBank accession numbers for nrITS
Authors: Jin-Hong Dai, Qiu-Jie Zhou, Ren-Chao Zhou, Ying Liu
Data type: Table
Explanation note: Newly generated sequences are indicated in bold.

Link: https://doi.org/10.3897/phytokeys.152.53512.suppl1

Supplementary material 2

Table S2. Summary statistics of sequences used for phylogenetic analyses
Authors: Jin-Hong Dai, Qiu-Jie Zhou, Ren-Chao Zhou, Ying Liu
Data type: Table
Explanation note: PIS, parsimony-informative sites.

Link: https://doi.org/10.3897/phytokeys.152.53512.suppl2

Supplementary material 3

Table S3. Pairwise genetic distances among species of *Bredia* at the nrITS region
Authors: Jin-Hong Dai, Qiu-Jie Zhou, Ren-Chao Zhou, Ying Liu
Data type: Table
Explanation note: Those between B. hispida and remaining species are indicated in bold.

Link: https://doi.org/10.3897/phytokeys.152.53512.suppl3

PhytoKeys 152: 15–25 (2020)
doi: 10.3897/phytokeys.152.51760
http://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
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Taxonomic studies on the genus *Isotrema* (Aristolochiaceae) from China: II. *I. brevilimbum* (Aristolochiaceae), a new species from Guizhou, China

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Academic editor: Elton John de Lirio | Received 5 March 2020 | Accepted 1 June 2020 | Published 3 July 2020

Citation: Wang J, Ya J-D, Liu C, Liu G, Cao F, Ma J-S, Zhu X-X (2020) Taxonomic studies on the genus *Isotrema* (Aristolochiaceae) from China: II. *I. brevilimbum* (Aristolochiaceae), a new species from Guizhou, China. PhytoKeys 152: 15–25. https://doi.org/10.3897/phytokeys.152.51760

Abstract

A new species of *Isotrema* was recently discovered from Guizhou, China and is here named as *I. brevilimbum*. It is most similar to *I. ovatifolium* and *I. wardianum*, but differs in the morphology of leaves and flowers. A detailed description for the new species, along with line drawings, photographs, as well as morphological comparisons with similar species, are provided. In addition, the distribution of *I. wardianum* in China is here confirmed.

Keywords

Aristolochia wardiana, morphology, subgenus *Siphisia*, taxonomy

Introduction

Isotrema Raf. (Aristolochiaceae), previously treated as a subgenus of *Aristolochia* L., was recently reinstated as an independent genus based on molecular and morphological evidence (Zhu et al. 2019a). It can be distinguished from *Aristolochia* by the following set of characters: perianth strongly curved, gynostemium 3-lobed, anthers paired on the outer surface of each gynostemium segment, and capsule dehiscing basipetally (Do et al. 2015a; Zhu et al. 2019a). Several new species of *Isotrema* have been found and described from China and its neighbouring countries during recent years (Liu and Deng 2009; Xu et al. 2011; Yao 2012; Huang et al. 2013, 2015; Wu et al. 2013, 2015; Do et al. 2014, 2015a, 2015b, 2015c, 2015d, 2016, 2017, 2019; Huong et al. 2014; Lu and Wang 2014; Ohi-Toma et al. 2014; Zhu et al. 2015, 2016, 2017a, 2017b, 2018, 2019b, 2019c; Gong et al. 2018; Yang et al. 2018; Li et al. 2019; Peng et al. 2019; Zhou et al. 2019; Cai et al. 2020a, 2020b). Currently, a total of 106 species have been reported from *Isotrema*, most of which are distributed in eastern and southern Asia, with some species further extended to northern and central America (Zhu et al. 2019a). China accommodates ca. 66 species, among which 55 species are endemic (Huang et al. 2003; Li et al. 2019; Peng et al. 2019; Zhou et al. 2019; Zhu et al. 2019a, 2019b, 2019c, 2019d; Cai et al. 2020a, 2020b).

During our recent field explorations to southern China, an unknown species of *Isotrema* was collected. Our subsequent examination of specimens from 39 public herbaria (A, BM, BR, CDBI, CSFI, CSH, E, EMA, GXMI, HAST, HENU, HHBG, HIB, HITBC, HNWP, IBK, IBSC, K, KYO, KUN, L, LBG, LE, NAS, NTUF, P, PE, PEM, SM, SNU, SYS, TAI, TI, W, WCU, WU, WUK, XYTC, YUKU; abbreviations follow Thiers 2020) and study of related literature (Hwang 1981, 1988; Ma 1989a, 1989b; Tao 1997; Huang et al. 2003; Do et al. 2015a; Do and Nghiem 2017; Yang et al. 2018; Zhu et al. 2019a, 2019d) suggested it to be a new species. Hereafter, we describe it as *I. brevilimbum* X.X.Zhu, Jun Wang & F.Cao. Moreover, *I. wardianum* (J.S. Ma) X.X. Zhu, S. Liao & J.S. Ma was recently published (Zhu et al. 2019a) based on its basionym *A. wardiana* J.S. Ma, previously only known from Myanmar and India (Ma 1989a), which was recently collected from Medog County, Tibet, and here its distribution in China is confirmed. Measurements and morphological characters of *I. brevilimbum*, *I. ovatifolium* and *I. wardianum* were made from both dried specimens and field observations of living plants, as well as including related literature. The morphological characters of the description follow Huang et al. (2003).

Taxonomy

Isotrema brevilimbum X.X.Zhu, Jun Wang & F.Cao, sp. nov.

urn:lsid:ipni.org:names:77209990-1
Figures 1, 2A–F, 3, 4A–C, 5

Type. China. Guizhou: Weining County, Jinzhong Town, 2226 m alt., 5 Aug 2018, X.X. Zhu et al. ZXX18217 (holotype: CSH–0172289!; isotypes: CSH!, KUN!).

Diagnosis. *Isotrema brevilimbum* is morphologically similar to *I. ovatifolium* (S.M. Hwang) X.X. Zhu, S. Liao & J.S. Ma and *I. wardianum* (J.S. Ma) X.X. Zhu, S. Liao

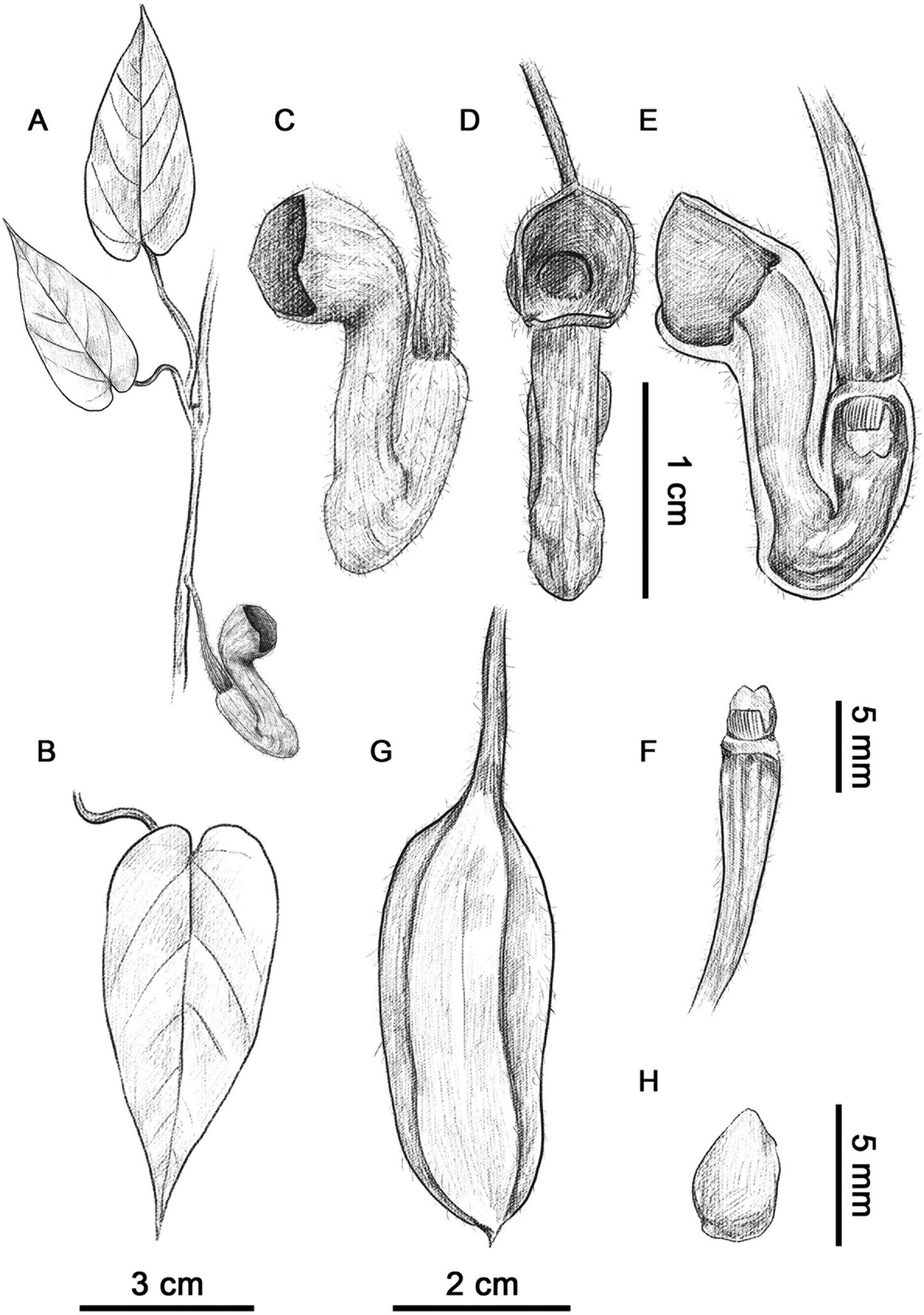

Figure 1. *Isotrema brevilimbum* X.X.Zhu, Jun Wang & F.Cao. **A** Branch **B** leaf **C, D** flower **E** longitudinal–section of flower (showing inside structure) **F** anthers and gynostemium **G** capsule **H** seed. Drawn by S.Z. Qiao.

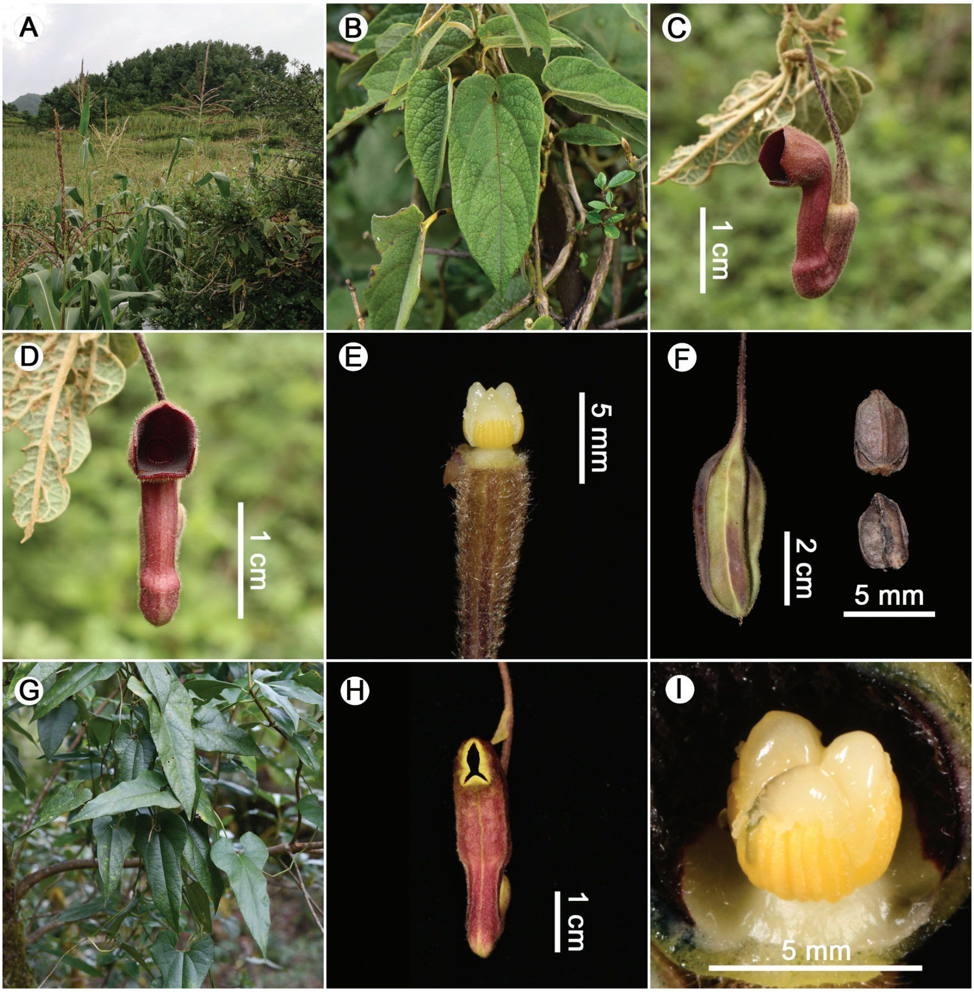

Figure 2. A–F *Isotrema brevilimbum* X.X.Zhu, Jun Wang & F.Cao. **A** Habitat **B** leaves **C** lateral view of flower **D** frontal view of flower **E** anthers and gynostemium **F** capsule **G–I** *I. wardianum* **G** habit **H** frontal view of flower **I** anthers and gynostemium. **A** Photographed by F. Cao **B, E, F** photographed by X.X. Zhu **C, D** photographed by G. Liu **G** photographed by C. Liu **H, I** photographed by J.D. Ya.

& J.S. Ma, but differs from the former in its lamina long ovate (vs. lamina ovate in *I. ovatifolium*), perianth limb forming right angle with upper tube, length nearly equal to width, and apex dark purple and opened (vs. limb straightly extended from upper tube, length significantly longer than width, and apex dark purple and constricted in *I. ovatifolium*), differs from the latter in its lamina long ovate and abaxially densely villous (vs. lamina lanceolate and abaxially subglabrous or glabrous in *I. wardianum*), perianth limb forming right angle with upper tube, length nearly equal to width, and apex dark purple and opened (vs. limb forming obtuse angle with upper tube, length significantly longer than width, and apex light yellow and constricted in *I. wardianum*).

上海辰山植物标本馆采集记录
Collect Record of the Shanghai Chenshan Herbarium

采集号 No. ZXX18217
采集人 Collector(s) 朱鑫鑫；王君；王志威；冯明旺
标本份数 Copy 3 日期 Date 20180805
俗名 Local name 短檐关木通
科名 Family Aristolochiaceae马兜铃科
学名 Species Isotrema brachylimitatum
产地 Location 贵州毕节市威宁彝族回族苗族自治县》金钟镇大岩山
经度 Lon. 104°26′00″ 纬度 Lat. 26°45′14″
分布 Frequency 海拔 Alt.(m) 2226m
生境 Habitat 亚热带，路边灌丛
基质 Substrate
性状 Habit 藤本 生活型 Life f.
体高 Height(m) 3－4m 胸径 Diam(cm)
根 Root 茎 Stem
叶 Leaf 花 Flower
果实 Fruit 种子 Seed
引种 Introduction
分子材料 Molecular sample
附记 Additinal

上海辰山植物标本馆鉴定记录
Determine Record of the Shanghai Chenshan Herbarium

No. 朱鑫鑫；王君；王志威；冯明旺 ZXX18217

Isotrema brachylimitatum X. X. Zhu, Jun Wang, F. Cao & J. S. Ma【短檐关木通】

鉴定人 Det. by 朱鑫鑫 鉴定日期 Det. Date Dec. 25. 2019

Figure 3. Holotype of *Isotrema brevilimbum* X.X.Zhu, Jun Wang & F.Cao (CSH–0172289).

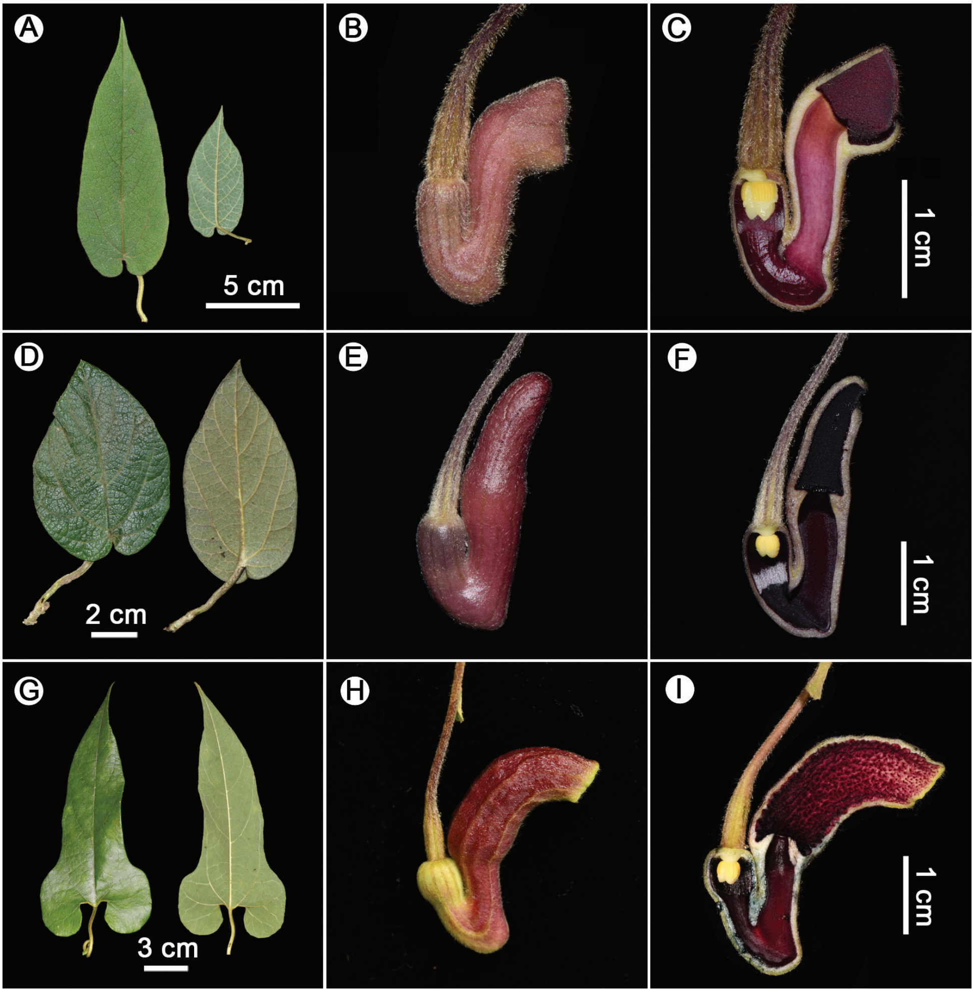

Figure 4. Leaves, lateral view of flowers, and longitudinal dissected flowers of *Isotrema brevilimbum* (**A–C**), *I. ovatifolium* (**D–F**), and *I. wardianum* (**G–I**). **A–F** Photographed by X.X. Zhu **G** photographed by C. Liu **H, I** photographed by J.D. Ya.

Description. Climbing shrubs. Stems terete, densely villous when young, old branchlets glabrous. Petioles 1–4 cm long, densely villous; laminas long ovate, 5–13 × 2.5–3.5 cm, adaxially appressed villous, abaxially densely villous, base cordate, margin entire, apex acute; basal veins palmate, 2–3 pairs from base, lateral veins 4–6-paired. Flowers axillary or lateral on young stems, solitary, rarely paired. Pedicels pendulous, 1.5–3 cm long, densely villous; bracteole ovate, conduplicate, ca. 2 × 1 mm, abaxially densely villous, adaxially smooth, inserted on lower part of pedicel. Perianth tube geniculately curved, abaxially villous; basal tube ca. 1 cm long, inside dark red, upper tube ca. 1.5 cm long, inside red; limb short cylinder, length nearly equal to width, ca. 7 × 8 mm, forming right angle with upper tube, apex dark purple, opened, ca. 7 mm wide at mouth, inside dark red with densely tiny dark-purple papillae; throat subcircular, ca. 4 mm wide. Anthers 6, oblong, ca.1.5 mm

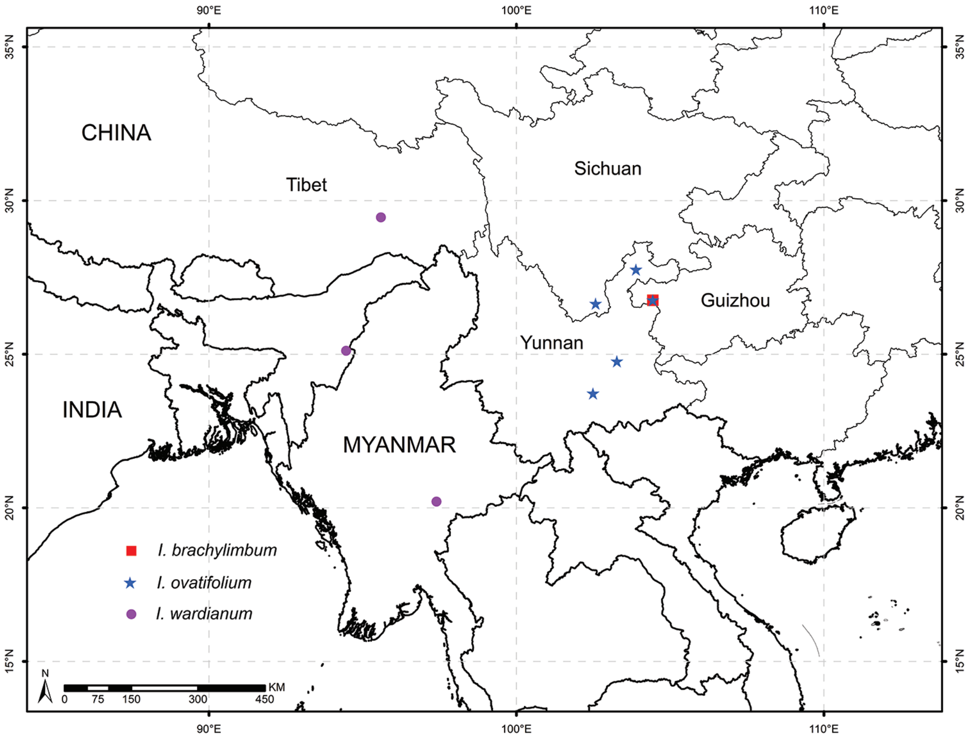

Figure 5. Distribution of *Isotrema brevilimbum*, *I. ovatifolium*, and *I. wardianum* based on field observation, specimens and literatures examined.

long, adnate in 3 pairs to base of gynostemium, opposite to lobes. Gynostemium ca. 3 mm long, 3-lobed. Ovary terete, ca. 8 mm long, densely villous. Capsule cylindric, abaxially densely villous, ca. 4.5 × 2 cm. Seeds ovate, 4–5 × 3–3.5 mm, concave-convex.

Phenology. Flowering from May to August, fruiting from July to September.

Etymology. The specific epithet refers to the short cylinder perianth limb of the new species. The "brevi" means "short", "limbum" means "limb", so the new species is named *Isotrema brevilimbum*.

Common name (assigned here). Duan Yan Guan Mu Tong (短檐关木通; Chinese name).

Distribution and habitat. The new species is currently only known from Weining County of Guizhou, China. It grows by the roadside of farmland at an altitude of ca. 2200 m.

Preliminary conservation status. *Isotrema brevilimbum* is known from a single population including two individuals on the roadside of farmland. The new species is assigned a preliminary status of vulnerable (VU) according to the IUCN Red List Categories (IUCN 2012). However, since very few details exist about its natural distribution, the lack of sufficient data currently does not allow a final risk evaluation and the species might be regarded as data deficient (DD). Further field surveys in western Guizhou and northeastern Yunnan are needed to gain more information on its distribution. Not only is the area not under protection as a nature reserve, but also habitat disturbance brought about by human activities, such as grazing and farming, may have a negative impact on the new species.

Note. *Isotrema wardianum* was previously only known from Myanmar and India. Sun and Zhou (2002) later reported the species from China, according to a specimen collected from Medog County of Tibet (*H. Sun et al. 4935*), but without flower or fruit. Nevertheless, the species had long been neglected by taxonomic studies of Huang et al. (2003), Do et al. (2015a), and Zhu et al. (2019a, 2019d) on Chinese *Isotrema*. It was not until 2018 that we discovered a seedling of *Isotrema* sp. at the same locality as that of *H. Sun et al. 4935* and transplanted it in the nursery of the Kunming Institute of Botany. A year later, the plant grown from this seedling bloomed and enabled us to identify it as *I. wardianum* (Figs 2G–I, 4G–I) and confirm its distribution in China.

Discussion

Isotrema brevilimbum is morphologically similar to *I. ovatifolium* and *I. wardianum* in the shape, size, and color of flower and the dark-purple papillae in the inner surface of perianth limb, but they can be distinguished by the morphology of lamina, the angle between perianth limb and upper tube, as well as the length and mouth of limb. Detailed morphological comparisons among the three species are summarized in Table 1 and Fig. 4.

Specimens of *Isotrema wardianum* examined. Myanmar. Adung Valley, 12 Apr 1931, F. Kingdon-Ward 9398 (holotype: BM). **China. Tibet:** Medog County, 2100 m, 21 Mar 1993, H. Sun et al. 4935 (KUN); **at the same locality**, 1705 m, 27 Nov 2018, C. Liu & J.D. Ya 18CS17145 (KUN).

Specimens of *Isotrema ovatifolium* examined. China. Guizhou: Weining County, Jinzhong Town, 2232 m, 5 Aug 2018, Zhu et al. ZXX18218 (CSH, KUN); **Sichuan:** Huidong County, 2520 m, 27 Jun 1959, S.K. Wu 1584 (type: SM).

Table 1. Morphological comparisons among *Isotrema brevilimbum*, *I. ovatifolium* and *I. wardianum*. These characters were based on field observation, related specimens and literatures (Hwang 1981; Ma 1989a; Huang et al. 2003).

Characters	*I. brevilimbum*	*I. ovatifolium*	*I. wardianum*
Lamina	long ovate, 5–13 × 2.5–3.5 cm, abaxially densely villous, base cordate	ovate, 5–13 × 4–8 cm, abaxially densely villous, base cordate	lanceolate, 12–16 × 3–4 cm, abaxially subglabrous or glabrous, base auriculate
Perianth limb	short cylinder, forming right angle with upper tube, length nearly equal to width, apex dark purple, opened, ca. 7 mm wide at mouth	cylinder, straightly extended from upper tube, length significantly longer than width, apex dark purple, constricted, ca. 1 mm wide at mouth	cylinder, forming obtuse angle with upper tube, length significantly longer than width, apex light yellow, constricted, ca. 3 mm wide at mouth
Perianth throat	ca. 4 mm wide	ca. 2.5 mm wide	ca. 2 mm wide
Anthers	ca. 1.5 mm long	ca. 1.5 mm long	ca. 2 mm long
Gynostemium	ca. 3 mm long	ca. 3.5 mm long	ca. 3.5 mm long
Capsule	ca. 4.5 × 2 cm	ca. 6 × 2 cm	unknown
Distribution	China (Guizhou)	China (Guizhou, Sichuan, Yunnan)	China, Myanmar, India

Acknowledgements

The authors are very grateful to Ms. Shi-Zhen Qiao for the line drawing of *I. brevilimbum*. This study was jointly supported by the National Natural Science Foundation of China (grant nos. 31600161 and 31370225), the Nanhu Scholars Program for Young Scholars of XYNU, and the Institute for Conservation and Utilization of Agro-bioresources in the Dabie Mountains.

References

Cai L, He DM, Huang YS, Dao ZL (2020a) *Aristolochia wenshanensis*, a new species of Aristolochiaceae from karst region in southeastern Yunnan, China. Taiwania 65(1): 41–46.

Cai L, Dao ZL, Zhu XX (2020b) *Isotrema hei* (Aristolochiaceae), a new species from southeastern Yunnan, China. Annales Botanici Fennici 57: 125–129. https://doi.org/10.5735/085.057.0117

Do TV, Nghiem TD (2017) Taxonomic notes on some *Aristolochia* species in Vietnam. Taiwania 62(2): 216–218.

Do TV, Luu TH, Wanke S, Neinhuis C (2015a) Three new species and three new records of *Aristolochia* subgenus *Siphisia* from Vietnam including a key to the Asian species. Systematic Botany 40(3): 671–691. https://doi.org/10.1600/036364415X689140

Do TV, Neinhuis C, Wanke S (2015b) A new species of *Aristolochia* subgenus *Siphisia* (Aristolochiaceae) from central Vietnam. Phytotaxa 220(1): 69–76. https://doi.org/10.11646/phytotaxa.220.1.6

Do TV, Nghiem TD, Wanke S, Neinhuis C (2014) *Aristolochia quangbinhensis* (Aristolochiaceae), a new species from Central Vietnam. PhytoKeys 33: 51–59. https://doi.org/10.3897/phytokeys.33.6094

Do TV, Nguyen DQ, Nguyen TQT, Wanke S, Neinhuis C (2015c) *Aristolochia cochinchinensis* (Aristolochiaceae), a new species from southern Vietnam. Annales Botanici Fennici 52(3–4): 268–273. https://doi.org/10.5735/085.052.0321

Do TV, Truong CQ, Huynh HTT (2017) *Aristolochia neinhuisii* (Aristolochiaceae), a new species from Vietnam. Annales Botanici Fennici 54(4–6): 203–208. https://doi.org/10.5735/085.054.0602

Do TV, Vu TTH, Luu HT, Nguyen TT (2019) *Aristolochia nuichuaensis* (subg. *Siphisia*, Aristolochiaceae), a New Species, an updated key and a checklist to the species of *Siphisia* in Vietnam. Annales Botanici Fennici 56(1–3): 107–113. https://doi.org/10.5735/085.056.0116

Do TV, Wanke S, Neinhuis C (2016) *Aristolochia bidoupensis* sp. nov. from southern Vietnam. Nordic Journal of Botany 34(5): 513–516. https://doi.org/10.1111/njb.01066

Do TV, Wanke S, Neinhuis C, Pooma R (2015d) *Aristolochia phuphathanaphongiana* sp. nov. from southwestern Thailand. Nordic Journal of Botany 33(5): 567–571. https://doi.org/10.1111/njb.00889

Gong QB, Landrein S, Xi HC, Ma XD, Yang ZH, He KW, Shen JY (2018) *Aristolochia tongbiguanensis*, a new species of Aristolochiaceae from Yunnan, China. Taiwania 63(3): 183–187.

Hwang SM (1981) Materials for Chinese *Aristolochia.* Zhiwu Fenlei Xuebao 19: 222–231.

Huang SM, Kelly LM, Gilbert MG (2003) *Aristolochia* Linnaeus. In: Wu ZY, Raven PH, Hong DY (Eds) Flora of China 5. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 258–269.

Huang YS, Peng RC, Tan WN, Wei GF, Liu Y (2013) *Aristolochia mulunensis* (Aristolochiaceae), a new species from limestone areas in Guangxi, China. Annales Botanici Fennici 50(3): 175–178. https://doi.org/10.5735/085.050.0308

Huang YS, Peng YD, Huang BY, Lv HZ, Lin CR (2015) *Aristolochia gongchengensis* (Aristolochiaceae), a new species from the limestone areas in Guangxi, China. Annales Botanici Fennici 52(5–6): 396–400. https://doi.org/10.5735/085.052.0522

Hwang SM (1988) *Aristolochia* Linnaeus. In: Kiu HS, Ling YR (Eds) Flora Reipublicae Popularis Sinicae 24. Science Press, Beijing, 199–245.

Huong NTT, Hai DV, Quang BH, Cuong NT, Khang NS, Vu DQ, Ma JS (2014) *Aristolochia xuanlienensis*, a new species of Aristolochiaceae from Vietnam. Phytotaxa 188(3): 176–180. https://doi.org/10.11646/phytotaxa.188.3.7

IUCN (2012) IUCN Red List Categories and Criteria, Version 3.1 (2nd Ed.) Gland and Cambridge, 32 pp.

Li RT, Wang ZW, Wang J, Zhu XX, Xu H (2019) *Isotrema sanyaense*, a new species of Aristolochiaceae from Hainan, China. PhytoKeys 128: 85–96. https://doi.org/10.3897/phytokeys.128.35042

Liu ZW, Deng YF (2009) *Aristolochia wuana*, a new name in Chinese *Aristolochia* (Aristolochiaceae). Novon 19(3): 370–371. https://doi.org/10.3417/2007151

Lu CT, Wang JC (2014) *Aristolochia yujungiana* (Aristolochiaceae): A new species from Taiwan. Taiwan Linye Kexue 29: 291–299.

Ma JS (1989a) A revision of *Aristolochia* Linn. from E. & S. Asia. Zhiwu Fenlei Xuebao 27: 321–364.

Ma JS (1989b) A revision of *Aristolochia* from Yunnan. Yunnan Zhi Wu Yan Jiu 11: 321–323.

Ohi-Toma T, Watanabe-Toma K, Murata H, Murata J (2014) Morphological variations of *Aristolochia kaempferi* and *A. tanzawana* (Aristolochiaceae) in Japan. Shokubutsu Kenkyu Zasshi 89: 152–163.

Peng YD, Gadagkar SR, Li J, Xie YY, Huang XY, Lu HZ, Huang BY, Yu LY (2019) *Aristolochia kechangensis* sp. nov (Aristolochiaceae) from Guangxi, China. Nordic Journal of Botany 37(9): e02456. https://doi.org/10.1111/njb.02456

Sun H, Zhou ZK (2002) Seed Plants of The Big Bend Gorge of Yalu Tsangpo in SE Tibet, E Himalayas. Yunnan Science & Technology Press, Kunming, 425 pp.

Tao DD (1997) Aristolochia Linnaeus. In: Chen SK (Ed.) Flora Yunnanica 8. Science Press, Beijing, 7–25.

Thiers B (2020) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's virtual Herbarium. http://sweetgum.nybg.org/ih/ [accessed 11 March 2020]

Wu L, Xu WB, Huang YS, Liu Y (2015) *Aristolochia longlinensis* (Aristolochiaceae), a new species from Western Guangxi, China. Novon 23(4): 490–493. https://doi.org/10.3417/2011105

Wu L, Xu WB, Wei GF, Liu Y (2013) *Aristolochia huanjiangensis* (Aristolochiaceae), a new species from Guangxi, China. Annales Botanici Fennici 50(6): 413–416. https://doi.org/10.5735/085.050.0608

Xu H, Li YD, Yang HJ, Chen HQ (2011) Two new species of *Aristolochia* (Aristolochiaceae) from Hainan Island, China. Novon 21(2): 285–289. https://doi.org/10.3417/2009116

Yang B, Ding HB, Zhou SS, Zhu XX, Li R, Mya BM, Tan YH (2018) *Aristolochia sinoburmanica* (Aristolochiaceae), a new species from north Myanmar. PhytoKeys 94: 13–22. https://doi.org/10.3897/phytokeys.94.21557

Yao TL (2012) *Aristolochia vallisicola* (Aristolochiaceae), a new species from Peninsular Malaysia. PhytoKeys 14: 15–22. https://doi.org/10.3897/phytokeys.14.3354

Zhou XX, Jiang GB, Zhu XX, Liu ZY, Huang Y, Wang GT, Wang RJ (2019) *Isotrema plagiostomum* (Aristolochiaceae), a new species from Guangdong, South China. Phytotaxa 405(4): 221–225. https://doi.org/10.11646/phytotaxa.405.4.7

Zhu XX, Li XQ, Liao S, Du C, Wang Y, Wang ZH, Yan J, Zuo YJ, Ma JS (2019a) Reinstatement of *Isotrema*, a new generic delimitation of *Aristolochia* subgen. *Siphisia* (Aristolochiaceae). Phytotaxa 401(1): 1–23. https://doi.org/10.11646/phytotaxa.401.1.1

Zhu XX, Li XQ, Liao S, Li GD, Ma JS (2019b) The taxonomic revision of Asian *Aristolochia* (Aristolochiaceae) V: Two new species from Yunnan, China. PhytoKeys 130: 93–106. https://doi.org/10.3897/phytokeys.130.33933

Zhu XX, Liao S, Zhang L, Wang ZH, Du C, Ma JS (2016) The taxonomic revision of Asian *Aristolochia* (Aristolochiaceae) I: Confirmation and illustration of *A. austroszechuanica A faucimaculata* and *A. yunnanensis* var. *meionantha* from China. Phytotaxa 261(2): 137–146. https://doi.org/10.11646/phytotaxa.261.2.3

Zhu XX, Liao S, Sun ZP, Zhen AG, Ma JS (2017a) The taxonomic revision of Asian *Aristolochia* (Aristolochiaceae) II: Identities of *Aristolochia austroyunnanensis A dabieshanensis* and *A. hyperxantha* – a new species from Zhejiang, China. Phytotaxa 313(1): 61–76. https://doi.org/10.11646/phytotaxa.313.1.4

Zhu XX, Liao S, Ma ZX, Xu B, Wang ZH, Wang Y, Ma JS (2017b) The taxonomic revision of Asian *Aristolochia* (Aristolochiaceae) III: Two new taxa of *Aristolochia* and morphological revision for the flower character of *A. obliqua* from Yunnan, China. Phytotaxa 332(3): 269–279. https://doi.org/10.11646/phytotaxa.332.3.3

Zhu XX, Shen B, Sun ZP, Chen B, Liao S, Ma JS (2018) Two New Species of *Aristolochia* (Aristolochiaceae) from Yunnan, China. Novon 26(3): 298–306. https://doi.org/10.3417/2018066

Zhu XX, Wang J, Liao S, Ma JS (2019d) Synopsis of *Aristolochia* L. and *Isotrema* Raf (Aristolochiaceae) in China. Shengwu Duoyangxing 27(10): 1143–1146. https://doi.org/10.17520/biods.2019183

Zhu XX, Zhang L, Hua ZX, Chen GF, Liao S, Ma JS (2015) *Aristolochia weixiensis*, a new species of Aristolochiaceae from Yunnan, China. Phytotaxa 230(1): 54–60. https://doi.org/10.11646/phytotaxa.230.1.4

Zhu XX, Zheng HL, Wang J, Gao YQ, Ma JS (2019c) Taxonomic studies on the genus *Isotrema* (Aristolochiaceae) from China: I. *I. cangshanense*, a new species from Yunnan. PhytoKeys 134: 115–124. https://doi.org/10.3897/phytokeys.134.37243

PhytoKeys 152: 27–104 (2020)
doi: 10.3897/phytokeys.152.49604
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RESEARCH ARTICLE

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The concluding chapter: recircumscription of *Goodenia* (Goodeniaceae) to include four allied genera with an updated infrageneric classification

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Academic editor: C. Morden | Received 23 December 2019 | Accepted 30 March 2020 | Published 7 July 2020

Citation: Shepherd KA, Lepschi BJ, Johnson EA, Gardner AG, Sessa EB, Jabaily RS (2020) The concluding chapter: recircumscription of *Goodenia* (Goodeniaceae) to include four allied genera with an updated infrageneric classification. PhytoKeys 152: 27–104. https://doi.org/10.3897/phytokeys.152.49604

Abstract

Close scrutiny of *Goodenia* (Goodeniaceae) and allied genera in the 'Core Goodeniaceae' over recent years has clarified our understanding of this captivating group. While expanded sampling, sequencing of multiple regions, and a genome skimming reinforced backbone clearly supported *Goodenia s.l.* as monophyletic and distinct from *Scaevola* and *Coopernookia*, there appears to be no synapomorphic characters that uniquely characterise this morphologically diverse clade. Within *Goodenia s.l.*, there is strong support from nuclear, chloroplast and mitochondrial data for three major clades (Goodenia Clades A, B and C) and various subclades, which lead to earlier suggestions for the possible recognition of these as distinct genera. Through ongoing work, it has become evident that this is impractical, as conflict remains within the most recently diverged Clade C, likely due to recent radiation and incomplete lineage sorting. In light of this, it is proposed that a combination of morphological characters is used to circumscribe an expanded *Goodenia* that now includes *Velleia*, *Verreauxia*, *Selliera* and *Pentaptilon*, and an updated infrageneric classification is proposed to accommodate monophyletic subclades. A total of twenty-five new combinations, three reinstatements, and seven new names are published herein including *Goodenia* subg. *Monochila* sect. *Monochila* subsect. *Infracta* K.A.Sheph. **subsect. nov.** Also, a type is designated for *Goodenia* subg. *Porphyranthus* sect. *Ebracteolatae* (K.Krause) K.A.Sheph. **comb. et stat. nov.**, and lectotypes or secondstep lectotypes are designated for a further three names.

Keywords

Goodenia, Goodeniaceae, nomenclature, phylogeny, taxonomy, *Velleia*

Introduction

Representatives of the predominantly Australian family Goodeniaceae R.Br, a close relative to the cosmopolitan Asteraceae Bercht. & J.Presl (Tank and Donoghue 2010), have been the focus of various studies in recent years. The first molecular phylogeny of generic exemplars by Gustafsson et al. (1996) indicated that the monotypic and closely allied Brunoniaceae Dumort. was, in fact, embedded within Goodeniaceae. This was previously hypothesised by Carolin (1992a), due to the shared presence of a unique cup-like pollen presenter positioned at the apex of the style referred to as an indusium (Carolin 1960). Howarth et al. (2003) (and later expanded in Jabaily et al. 2014), studied the origin of Hawaiian species of *Scaevola* L., the only genus in the family with significant diversity outside of Australia (see table 1 in Jabaily et al. 2012). These studies confirmed that *Scaevola* dispersed from Australia into the islands of the Pacific at least four times, starting in the late Miocene and continuing into the Pliocene, and that homoploid hybridisation subsequently contributed to the extant diversity apparent across the islands today (Howarth and Baum 2005).

Our team completed the first comprehensive phylogeny of the family utilising cpDNA from 212 (out of 400+) species across 12 genera (Jabaily et al. 2012). Two major clades were identified within the family, the smaller of the two being the LAD clade composed of *Lechenaultia* R.Br., *Anthotium* R.Br., and *Dampiera* R.Br. with the remaining nine genera falling in the larger 'Core Goodeniaceae' clade (Fig. 1). Within the Core Goodeniaceae the monotypic *Brunonia australis* Sm. ex R.Br. placed sister to two large clades comprising *Scaevola s.l.* and *Goodenia* Sm. *s.l.,* respectively. Generic-level taxonomic problems were noted in both clades. Firstly, the monotypic *Diaspasis filifolia* R.Br. was shown to be embedded within *Scaevola* while *Goodenia s.l.* (represented by a subset of 60 species), resolved into three major clades (denoted A, B, C), and was rendered paraphyletic due to the inclusion of *Coopernookia* Carolin, *Selliera* Cav. (Fig. 2I), *Velleia* Sm. (Fig. 2E), *Verreauxia* Benth., *Scaevola collaris* F.Muell. (Fig. 2B) and the monotypic *Pentaptilon* E.Pritz. This phylogeny was built using 3117 base-pairs of cpDNA including *trnL-F* and *matK*, and while phylogenetic support values were high for many smaller clades, the backbone topology of *Goodenia s.l.* was weakly supported in most analyses. A few subgeneric taxonomic groupings were largely monophyletic (e.g. subg. *Monochila* (G.Don) Carolin, subg. *Goodenia* subsect. *Ebracteolatae* K.Krause), but many were not (e.g. subg. *Goodenia* subsect. *Goodenia* and subsect. *Coeruleae* (Benth.) Carolin). Furthermore, other subgeneric groupings were not included or placed (e.g. sect. *Porphyranthus* G.Don, sect. *Amphichila* DC., and ser. *Calogyne* (R.Br.) Carolin of subg. *Goodenia*).

Clarifying the relationships among *Goodenia* clades A, B, C and the smaller affiliate genera was necessary in order to identify monophyletic groups for taxonomic

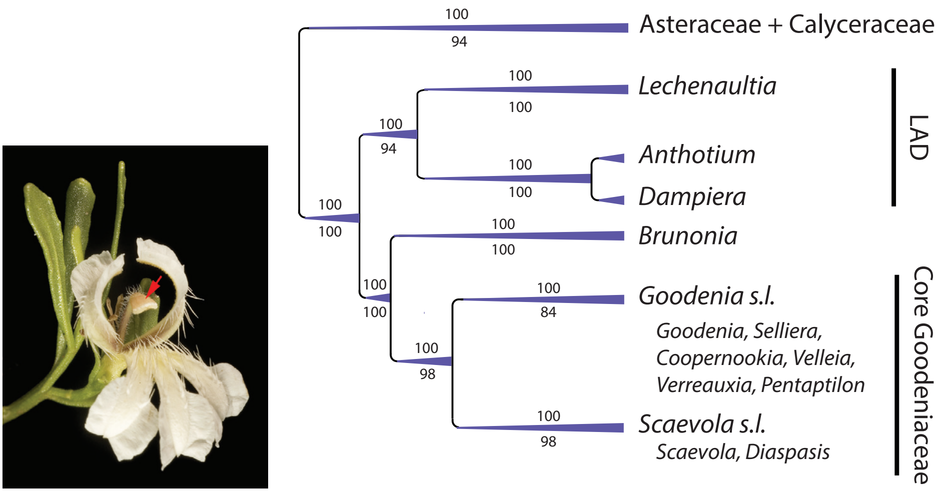

Figure 1. Summary of broad relationships in Goodeniaceae from Jabaily et al. (2012) based on a 50% majority-rule cladogram from a partitioned Bayesian inference analysis of *trnL-F* and *matK*, with additional bootstrap values from separate parsimony and maximum likelihood analyses (values above branches are Bayesian posterior probabilities, values below branches are maximum likelihood bootstrap). Left inset – *Coopernookia strophiolata* showing the unique indusium pollen presenter (red arrow) that is diagnostic for the family. Voucher: *K.R. Thiele* 3710. Image: K.R. Thiele.

recognition. We could not seek to make changes to *Goodenia s.l.* without, at minimum, full and consistent resolution of the backbone relationships and confidence in the species-level composition of each major clade. To try and address this issue, the power of next-generation sequencing was leveraged for a subset of taxa (Gardner et al. 2016a). Twenty-four taxa representative of almost all major clades within Core Goodeniaceae, including 19 accessions from *Goodenia s.l.* (except subsect. *Scaevolina* and a subset of species from subsect. *Goodenia* placed in Clade C), were sequenced using genome-skimming technology. The majority of coding regions of the chloroplast genome were assembled and analysed, resulting in a nearly fully resolved phylogeny for all but two nodes within *Goodenia s.l.* This topology was then applied as a constraint and also concatenated on an expanded matrix of 98 Core Goodeniaceae species with *trnL-F* and *matK* loci of sequence data, greatly improving phylogenetic support values. This backbone topology has been similarly utilised in the present study. The analyses of Gardner et al. (2016a) confirmed the position of *Coopernookia* as sister to the remainder of *Goodenia s.l.*, followed by stepwise sisters Clade A, Clade B, and finally *Velleia* sister to Clade C. However, the composition and relationships of subclades within the most morphologically diverse Clade C were poorly resolved, except for the monophyly of subg. *Monochila* and subg. *Goodenia* subsect. *Coeruleae*. Exploration of the backbone phylogeny derived from additional genomic compartments (nuclear ribosomal complex, several single copy nuclear genes) in the study suggested alternative topologies compared to the plastid, though with low support.

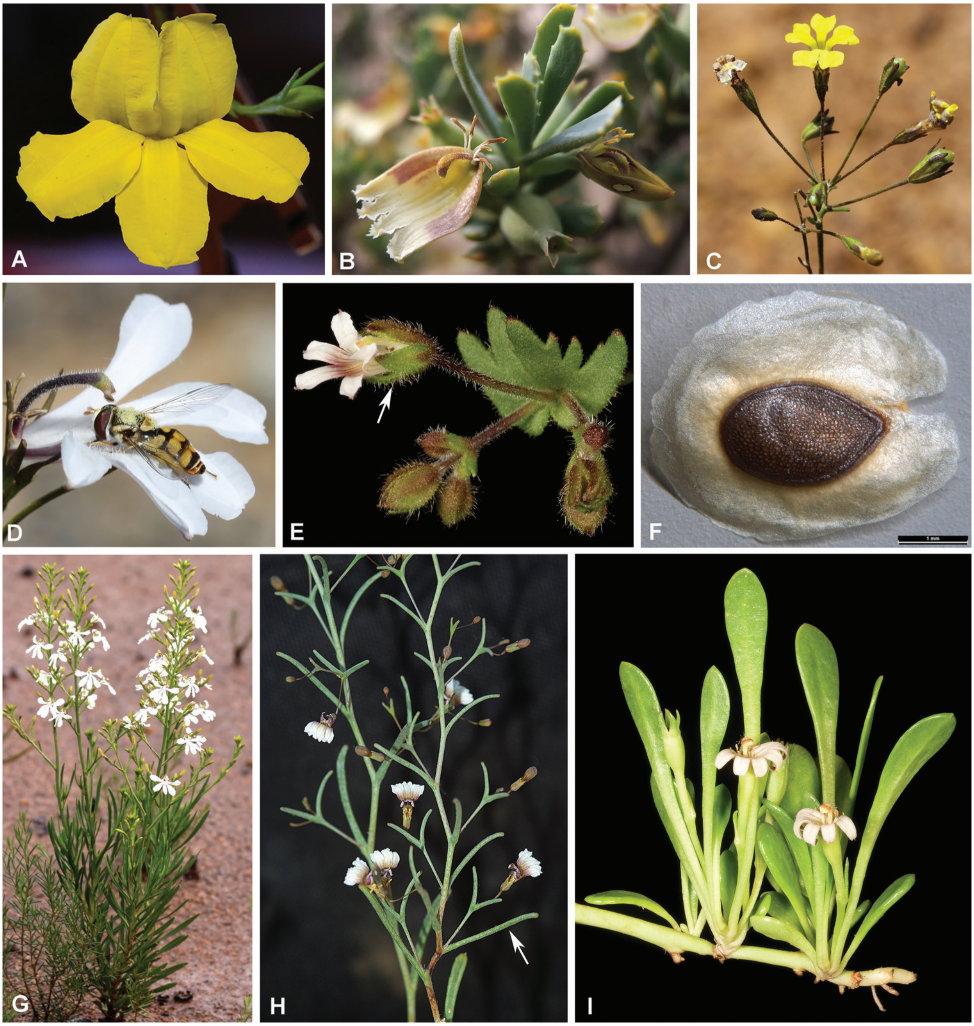

Figure 2. Diagnostic features of various species in *Goodenia s.l.* **A** the type species *Goodenia ovata* **B** *Scaevola collaris* fan-like flowers and immature fleshy fruit **C** *G. concinna* subumbellate inflorescence **D** *G. scapigera* with short, stiff hairs on the style, narrow indusium and white fan-like flowers **E** *Velleia cycnopotamica* with free sepals attached below the ovary (white arrow) **F** *G. vilmoriniae* seed with a broad membranous wing **G** *G. scapigera* habit with cauline leaves and thyrse-like inflorescences **H** *G. gypsicola* leafy bracts (white arrow) **I** *Selliera radicans* with prostrate stems rooting at the nodes, and solitary, bracteolate, fan-like flowers in the leaf axils. Vouchers: *K.A. Shepherd* KS 1530 (**A**); *K.A. Shepherd* KS 1533 (**B**); *K.A. Shepherd* KS 1591 (**C**); *K.A. Shepherd* KS 1584 (**D**); *K.R. Thiele* KRT 4201 (**E**); DEM6887 (**F**); *K.A. Shepherd* KS 1468 (**G**); *R. Davis s.n.*(**H**); *J.A. Cochrane & S. Barrett* 4181 (**I**). Images: K.A. Shepherd (**A–D, G**); K.R. Thiele (**E, I**); Seeds of South Australian (**F**); R. Davis (**H**).

To continue our investigation of alternative backbone topologies and delve into the poorly resolved Clade C, we expanded and further explored the next-generation sequencing data across nuclear, chloroplast and mitochondrial genomic compartments (Jabaily et al. 2018). We generated new genome skimming data for four additional taxa from within Clade C, and re-analysed the previously generated raw genomic data for the taxa in clade *Goodenia s.l.*, for a total of 24 taxa. Partial mitochondrial genomes and partial chloroplast genomes expanded beyond the efforts of Gardner et al. (2016a) similarly strongly supported our original backbone relationship within *Goodenia s.l.* Extensive hypothesis tests were performed to explore congruencies and determine statistical support for all possible relationships within the challenging Clade C. Still, relationships between taxa and subclades within Clade C remained poorly resolved with both mitochondrial and plastid loci, as well as an expanded nuclear data set. In conclusion, while there was strong support for the monophyly of subg. *Monochila* and all other subclades represented distinct lineages, their position relative to each other remained unresolved, thus precluding their recognition as well-supported genera.

Morphology of Core Goodeniaceae

The *Flora of Australia* treatment of Goodeniaceae and Brunoniaceae (Carolin 1992a; Carolin et al. 1992) represented more than 30 years of research by Roger Carolin and his students. Over this period, Carolin's team successively revised each genus through a series of detailed anatomical and morphological studies that culminated in the recognition of numerous new species and updated infrageneric classifications. Through his early cladistics work and study of inflorescence types, Carolin determined that there were two distinct assemblages within the Goodeniaceae (Carolin 1967a; Carolin 1977). The first was the *Lechenaultia-Anthotium-Dampiera* (LAD) group, united by the presence of a cymo-paniculate inflorescence, connate anthers and a base chromosome number × = 9. In contrast, the remaining genera within the '*Goodenia* group' had a fundamentally different vascularisation of the ovary, a thyrse or raceme-like inflorescence (Figs 2G, 3, 4), free anthers, and a base chromosome number of × = 7 or 8. These broad relationships were borne out in subsequent molecular studies (Jabaily et al. 2012; Gardner et al. 2016a) (Fig. 1). Carolin (1992a) rightly pointed out that *Brunonia* was clearly allied to the LAD group and perhaps should not be supported as a distinct family; however, Brunoniaceae was ultimately retained for his *Flora of Australia* treatment due to the adoption of the Cronquist (1981) classification system by the *Flora* at its inception (Kanis 1981). Within his '*Goodenia* group', Carolin (1977) also determined that the monotypic south-west Western Australian genus *Diaspasis* was allied to *Scaevola* despite the presence of connate anthers and almost radially symmetrical flowers compared to the free anthers and fan-shaped flowers typical of the widely distributed *Scaevola* (Carolin 1992c; 1992d); a relationship subsequently confirmed through phylogenetic analyses (Jabaily et al. 2012). Finally, Carolin (1990; 1992e) concluded that *Coopernookia*, *Velleia*, *Verreauxia*, and *Pentaptilon* were allied to *Goodenia*, along with the four genera *Calogyne* R.Br., *Symphyobasis* K.Krause, *Neogoodenia* C.A.Gardner & A.S.George, and *Catosperma* Benth. that were later subsumed into an expanded *Goodenia*.

Coopernookia is the only genus in the family that shows the classic SW–SE Australian disjunction from the Nullarbor uplift around 8.8 to 0.5 million years ago (Jabaily et al. 2014), with three species endemic to the central and south west of the continent

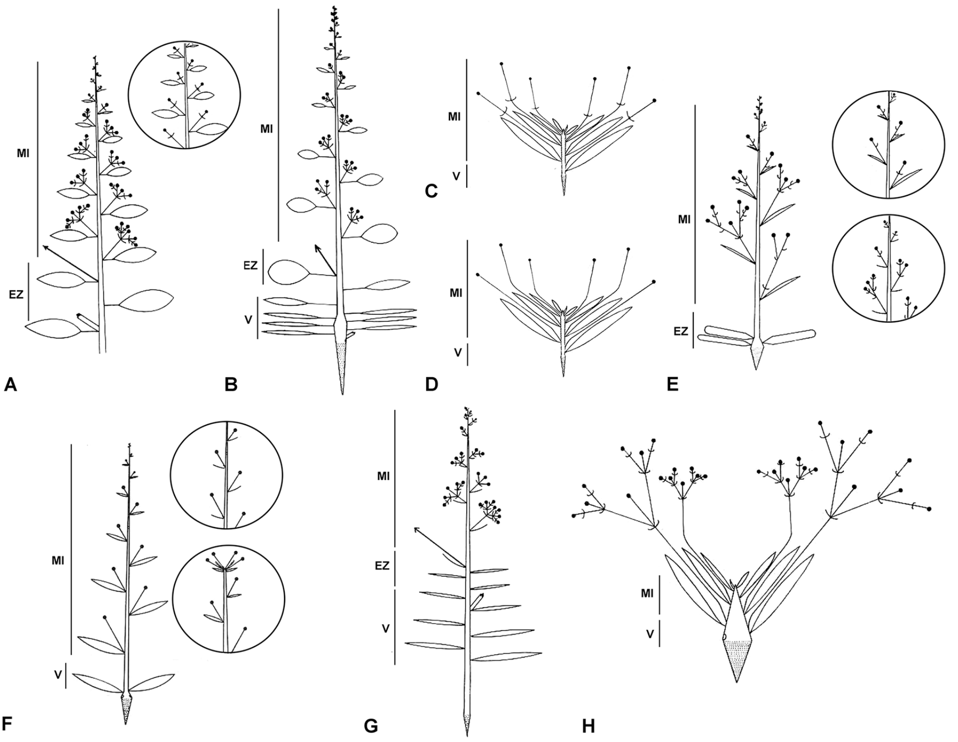

Figure 3. Characterisation of inflorescence structure in *Goodenia s.l.* modified from Carolin (1967a) with his corresponding Bauplan 'Type' concepts stated were applicable and phylogenetic position for exemplar species given in brackets; MI = main inflorescence, EZ = enrichment zone, V = vegetative zone. **A** Form A (Type 1) is a thyrse with leafy bracts and bracteoles e.g. *Goodenia ovata* (Goodenia I) or (Type 2) 1(–2)-flowered raceme with leafy bracts and bracteoles e.g. *G. laevis* (Goodenia I) (inset) **B** Form B (Type 5) is a basal rosette with leafy bracts and bracteoles e.g. *G. hederacea* (Goodenia II) **C** Form C (no Type) with flowers solitary in leaf axils, leafy bracts and bracteoles e.g. *G. convexa* (Goodenia II) **D** Form D (no Type) flowers solitary in leaf axils with leafy bracts, bracteoles absent e.g. *G. pumilo* (Porphyranthus I) **E** Form E (Type 4) a basal rosette, bracteoles, with leafy bracteose bracts and either a panicle-like form e.g. *G. paniculata*, raceme e.g. *G. gracilis* (Porphyranthus II) (inset above) or a thyrse e.g. *G. pterigosperma* (Coeruleae) (inset below) **F** Form F (Type 6) with ebracteolate racemes and leafy bracts e.g. *G. hispida* (Ebracteolatae II), (Type 7) non-leafy bracts e.g. *G. cusackiana* (Ebracteolatae I) (inset above), or (Type 8) a subumbel e.g. *G . pulchella* (Ebracteolatae I) (inset below) **G** Form G (Type 3) represented by a thyrse with reduced bracts and bracteoles e.g. *G. scapigera* (Monochila) and **H** Form H (Velleia Type) is a compound dichasium with leafy bracts and bracteoles e.g *Velleia lyrata* (Velleia).

and three confined to eastern Australia (Carolin 1992b). Carolin (1967b) recognised this genus as distinct from the rest of his '*Goodenia* group' as all species have a base chromosome number of × = 7 (rather than 8), stellate hairs on the stems and leaves, and ovoid, strophiolate seeds. The seed testa is also unique, with thickened, straight-sided cell walls that contain no mucilage in contrast to many species of *Goodenia* that

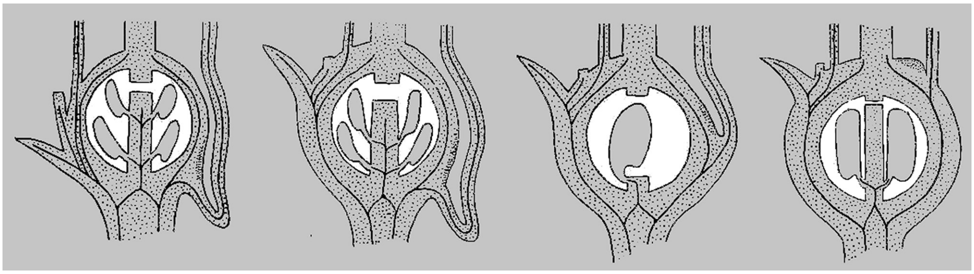

Figure 4. Diagramatic sections of ovaries (l.s.) modified from Carolin (1959). From left–right *Velleia*, *Goodenia*, *Verreauxia*, and *Scaevola*, showing fusion of floral parts and structure of the incomplete locules and placentation of ovules.

have somewhat compressed seeds, where the epidermal cells are thickened towards the centre and thinner towards the margins and may contain mucilage that swells when wet (Carolin 1966). The flowers of *Coopernookia* also have retrorse barbulae inside the corolla that act as pollinator guides, reminiscent to those present in *Scaevola*. Indeed, Carolin (1967b) insightfully postulated that *Coopernookia* would have an intermediate position between *Scaevola* and *Goodenia*, which was later supported by molecular data as it was shown to be sister to *Goodenia s.l.* (Gardner et al. 2016a).

Goodenia is the largest and most floristically diverse genus in Goodeniaceae with c. 220 species. Species are largely confined to Australia apart from a few representatives that extend northwards to New Guinea, Indonesia, Malaysia, Philippines, and China, with a single taxon also endemic to the Island of Java (Leenhouts 1957; Carolin 1992e; Hong and Howarth 2011). *Goodenia* are annual or perennial herbs or low shrubs that occupy a wide variety of habitats in almost every biome across the Australian continent. Many species have yellow, white or blue bilabiate flowers (Figs 2, 5–8), although there have been multiple independent floral symmetry shifts to a fan-shaped flower form (Gardner et al. 2016b). Fruit structure, seed coat surface patterns and appendages such as wings (Fig. 2F) are also important diagnostic characters for the genus (Carolin 1980). Recently, it was determined that the genus *Goodenia* had been lectotypified incorrectly as the first named species, *G. ramosissima* Sm., is in fact a species of *Scaevola* (≡ *S. ramosissima* (Sm.) K.Krause). Consequently, a proposal was put forward to conserve the name *Goodenia* using the conserved type *G. ovata* Sm. (Shepherd et al. 2017) (Fig. 2A), which was subsequently accepted (Applequist 2019). Carolin's (1992e) infrageneric classification currently recognises two subgenera and various sections, subsections and series (Table 1).

Selliera, a genus of three fan-flowered species from Australia, New Zealand and Chile, was supported as distinct within Carolin's (1977) '*Goodenia* group'. However, he later questioned its status (Carolin 1992f), noting that these species resembled members of *Goodenia* sect. *Goodenia* with fruits that show "a striking resemblance to that of *G. koningsbergeri* (Backer) Backer ex Bold. although somewhat smaller" (Carolin 1966), and he suggested that future work may determine that *Selliera* should be

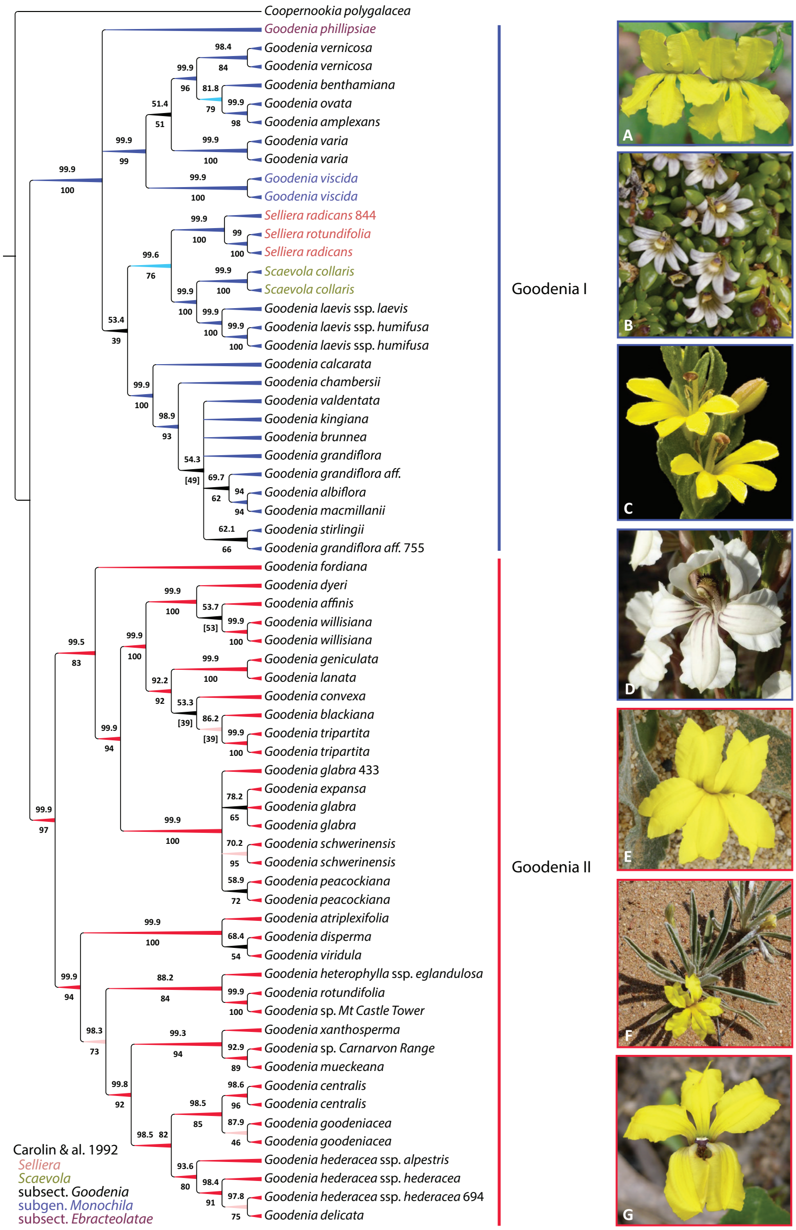

Figure 5. *Goodenia* Clade A phylogeny from combined nrDNA + cpDNA sequence data and exemplar taxa of major subclades. Topology is 50% majority rule cladogram from the partitioned Bayesian inference analysis. Support values above the branches are Bayesian posterior probabilities and below are maximum likelihood bootstrap values. Branch colour corresponds with support values and taxon colour corresponds to the taxonomic classification of Carolin et al. (1992). For updated taxonomy from this paper, see Tables 1, 2. Taxa represented by multiple accessions are distinguished by project code numbers as listed in Suppl. material 1. **A** *G. ovata* **B** *Selliera radicans* **C** *G. viscida* **D** *G. calcarata*; **E** *G. tripartita* **F** *G. willisiana* **G** *G. hederacea*. Images: J. Tann (**A, G**); R. Cumming (**B**); K.R. Thiele (**C**); Seeds of South Australia (**D, F**); K.A. Shepherd (**E**).

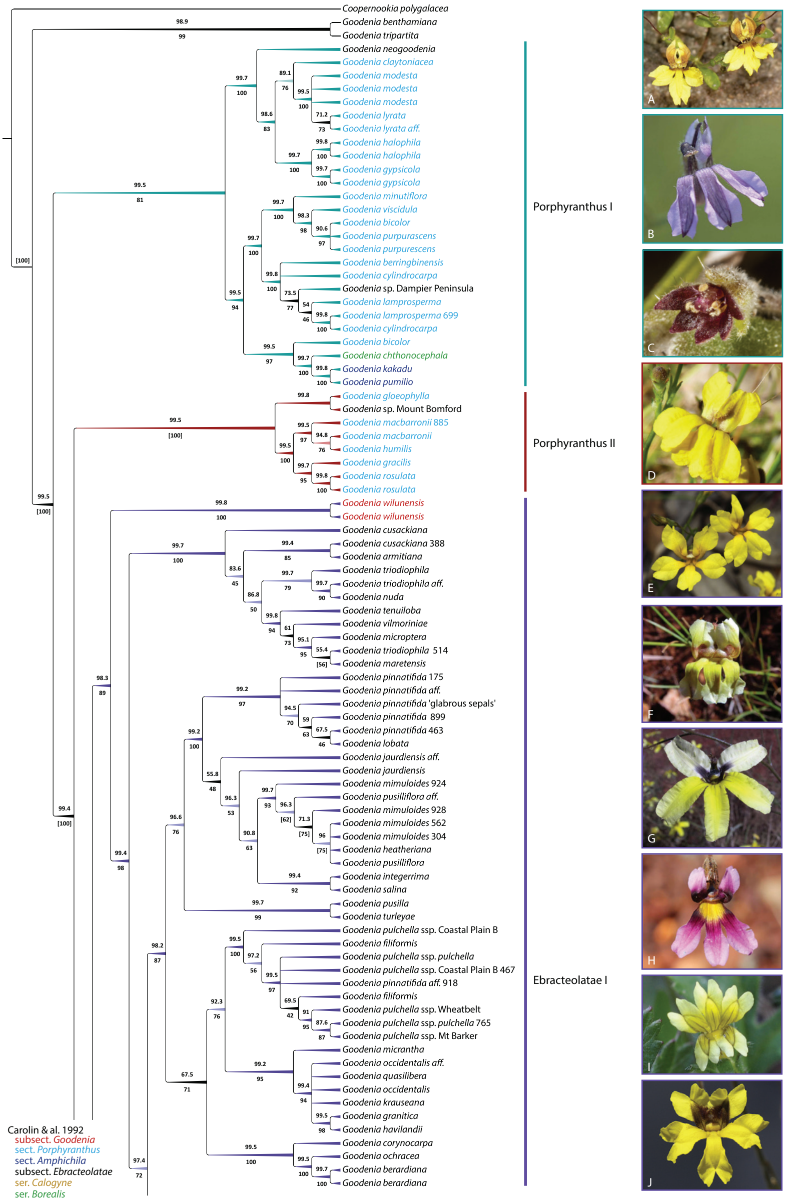

Figure 6. *Goodenia* Clade B_1 phylogeny from combined nrDNA + cpDNA sequence data and exemplar taxa of major subclades. Topology is 50% majority rule cladogram from the partitioned Bayesian inference analysis. Support values above the branches are Bayesian posterior probabilities and below are maximum likelihood bootstrap values. Branch colour corresponds with support values and taxon colour corresponds to the taxonomic classification of Carolin et al. (1992). For updated taxonomy from this paper, see Tables 1, 2. Taxa represented by multiple accessions are distinguished by project code numbers as listed in Suppl. material 1. **A** *G. claytoniacea* **B** *G. purpurascens* **C** *G. pumilio* **D** *G. macbarronii* **E** *G. pinnatifida* **F** *G. nuda* **G** *G. tenuiloba* **H** *G. vilmoriniae* **I** *G. pusilliflora* **J** *G. occidentalis*. Images: F. & J. Hort (**A**); C. Nieminski (**B**); R.L. Barrett (**C**); N. Blair (**D**); K.A. Shepherd (**E, J**); A. Perkins (**F, G**); R. Fryer & J. Newland (**H**); A. Gardner (**I**).

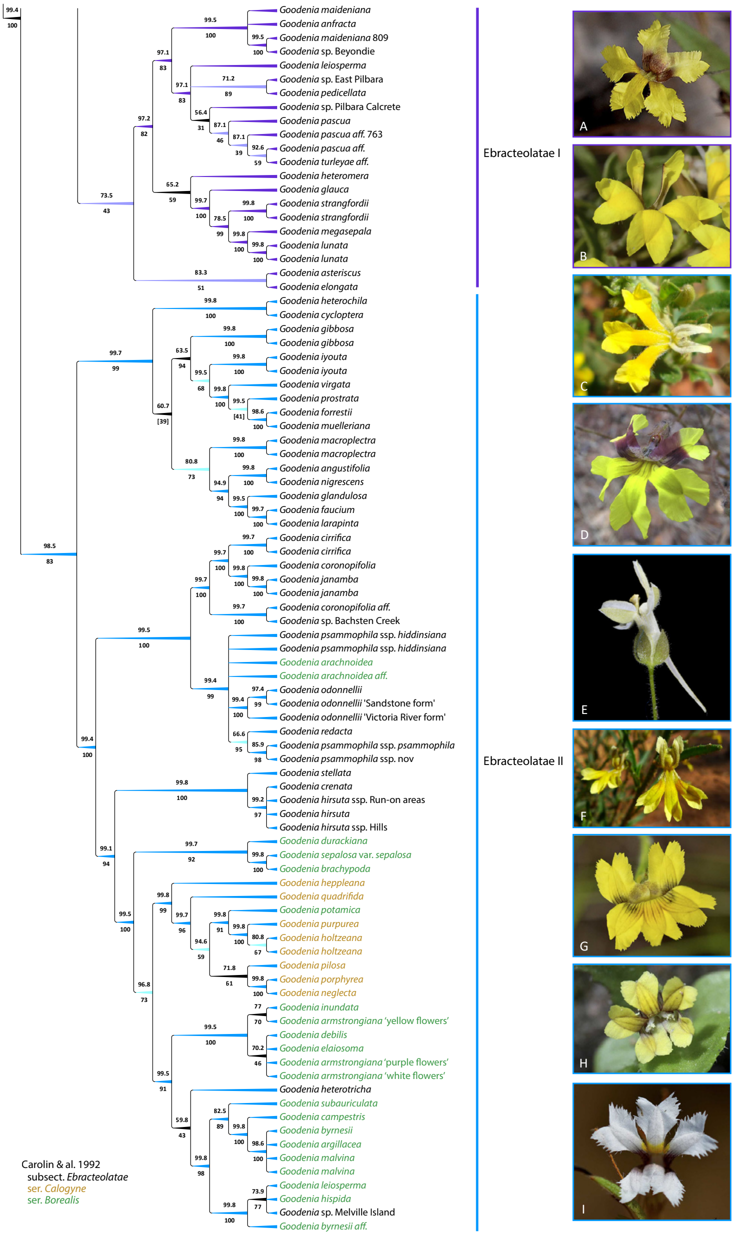

Figure 7. *Goodenia* Clade B_2 phylogeny from combined nrDNA + cpDNA sequence data and exemplar taxa of major subclades. Topology is 50% majority rule cladogram from the partitioned Bayesian inference analysis. Support values above the branches are Bayesian posterior probabilities and below are maximum likelihood bootstrap values. Branch colour corresponds with support values and taxon colour corresponds to the taxonomic classification of Carolin et al. (1992). For updated taxonomy from this paper, see Tables 1, 2. Taxa represented by multiple accessions are distinguished by project code numbers as listed in Suppl. material 1. **A** *G. leiosperma* **B** *G. heteromera* **C** *G. heterochila* **D** *G. muelleriana* **E** *G. macroplectra* **F** *G. glandulosa* **G** *G. odonnellii* **H** *G. pilosa* **I** *G. armstrongiana* (White form). Images: C. Nieminski (**A, G–I**); Seeds of South Australia (**B, C, F**); A. Perkins (**D**); K.R. Thiele (**E**).

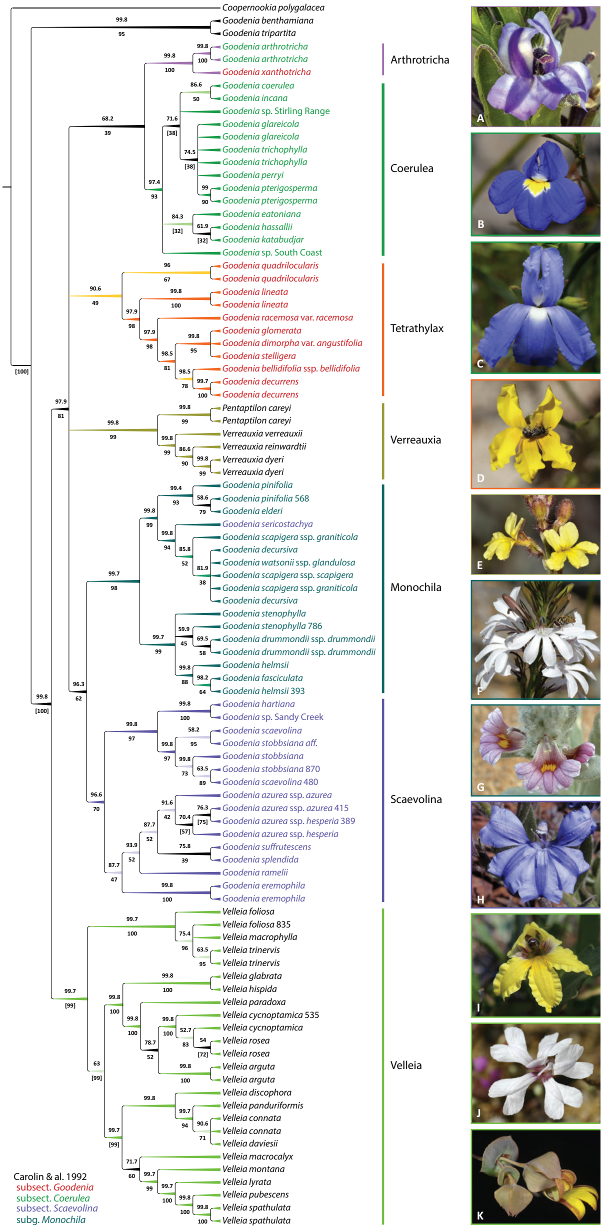

Figure 8. *Goodenia* Clade C phylogeny from combined nrDNA + cpDNA sequence data and exemplar taxa of major subclades. Topology is 50% majority rule cladogram from the partitioned Bayesian inference analysis. Support values above the branches are Bayesian posterior probabilities and below are maximum likelihood bootstrap values. Branch colour corresponds with support values and taxon colour corresponds to the taxonomic classification of Carolin et al. (1992). For updated taxonomy from this paper, see Tables 1, 2. Taxa represented by multiple accessions are distinguished by project code numbers as listed in Suppl. material 1. **A** *G. xanthotricha* **B** *G. coerulea* **C** *G. hassallii* **D** *G. quadrilocularis* **E** *Verreauxia reinwardtii* **F** *G. helmsii* **G** *G. sericostachya* **H** *G. stobbsiana* **I** *Velleia paradoxa* **J** *V. rosea* **K** *V. connata*. Images: A. Crawford (**A**); F. & J. Hort (**B, E–G**); K.A. Shepherd (**C, D, I, J**); A. Perkins (**H**); K.R.Thiele (**K**).

Table 1. Revised classification of *Goodenia s.l.* comparing the *Flora of Australia* treatment by Carolin (1992e) to an expanded *Goodenia* circumscribed herein that includes the genera *Selliera*, *Verreauxia*, *Pentaptilon* and *Velleia*, with the updated infrageneric classification and new authorities also provided.

Clade	**Carolin et al. (1992)**					**Shepherd et al.**		
	Genus	**subgenus**	**section**	**subsection**	**series**	**Subgenus**	**Section**	**Subsection**
Clade A	*Goodenia*	*Goodenia*	*Goodenia*	*Goodenia*		*Goodenia*	*Goodenia* [including *Selliera*]	
	Goodenia	*Goodenia*	*Goodenia*	*Goodenia*		*Goodenia*	*Rosulatae* (K.Krause) K.A.Sheph.	
Clade B	*Goodenia*	*Goodenia*	*Porphyranthus*			*Porphyranthus* (G.Don) K.A.Sheph.	*Porphyranthus*	
	Goodenia	*Goodenia*	*Amphichila*			*Porphyranthus* (G.Don) K.A.Sheph.	*Porphyranthus*	
	Goodenia	*Goodenia*	*Goodenia*	*Ebracteolatae*		*Porphyranthus* (G.Don) K.A.Sheph.	*Ebracteolatae* (K.Krause) K.A.Sheph.	
	Goodenia	*Goodenia*	*Goodenia*	*Borealis*	*Borealis*	*Porphyranthus* (G.Don) K.A.Sheph.	*Ebracteolatae* (K.Krause) K.A.Sheph.	
	Goodenia	*Goodenia*	*Goodenia*	*Borealis*	*Calogyne*	*Porphyranthus* (G.Don) K.A.Sheph.	*Ebracteolatae* (K.Krause) K.A.Sheph.	
Clade C	*Goodenia*	*Monochila*				*Monochila*	*Monochila*	*Monochila* (G.Don) K.A.Sheph.
	Goodenia	*Monochila*				*Monochila*	*Monochila*	*Infracta* K.A.Sheph.
	Goodenia	*Goodenia*	*Coeruleae*	*Coeruleae*		*Monochila*	*Coeruleae*	
	Goodenia	*Goodenia*	*Coeruleae*	*Scaevolina*		*Monochila*	*Scaevolina* (Carolin) K.A.Sheph.	
	Goodenia	*Goodenia p.p.*	*Goodenia p.p.*			*Monochila*	*Tetrathylax*	
	Verreauxia					*Monochila*	*Verreauxia* (Benth.) K.A.Sheph.	
	Pentaptilon					*Monochila*	*Verreauxia* (Benth.) K.A.Sheph.	
	Velleia		*Velleia*			*Monochila*	*Velleia*	
	Velleia		*Menoceras*			*Monochila*	*Velleia*	
	Velleia		*Euthales*			*Monochila*	*Velleia*	

synonymised under *Goodenia*. This appears to be supported as a single representative of the genus, *Selliera radicans* Cav. (Fig. 2I), was shown to group with the unusual *Scaevola collaris* (Carolin 1992c) (Fig. 2B) and the fan-flowered *G. viscida* R.Br. (Fig. 5C) in *Goodenia* Clade A (Jabaily et al. 2012; Gardner et al. 2016a). Furthermore, *S. radicans* had been previously synonymised into *Goodenia* by Persoon (1805); however, subsequent workers had not taken up this proposed change.

Verreauxia, a small genus of three species from southwest Western Australia, is distinguished by unusual multi-cellular branched hairs and a unilocular ovary (Fig. 4 and Fig. 8E) that develops into an indehiscent, nut-like fruit with a single seed that (unusually) does not contain any mucilaginous cells in the seed coat testa (Carolin 1966, 1992i). Carolin (1977) also included this genus in his '*Goodenia* group' along with the closely allied monotypic *Pentaptilon*, which has similar branched hairs but is distinguished by its uniquely winged ovary and fruit (Carolin 1992h). *Pentaptilon* together with *Verreauxia* formed a monophyletic group in molecular analyses within the morphologically variable Goodenia Clade C (Gardner et al. 2016a; Jabaily et al. 2018).

Velleia, the final genus in Carolin's (1977) '*Goodenia* group', currently includes 21 species endemic to Australia except *V. spathulata* R.Br., which is also found in Malaysia, western New Guinea and the Louisiade Archipelago (Leenhouts 1957; Carolin 1992g). Many species within this genus have a distinctive inflorescence structure comprised of expanded axillary dichasia (Fig. 3H). Another important diagnostic feature for *Velleia* is the presence of a predominantly superior ovary with the sepals, corolla and stamens usually adnate to the base (Carolin 1992g) (Fig. 2E). In contrast, the remaining Core Goodeniaceae generally have inferior ovaries, except *G. macroplectra* (F.Muell.) Carolin; a species in *Goodenia* subsect. *Ebracteolatae* (Jabaily et al. 2012) that has free sepals inferior to the ovary while the corolla is fused to the apex (Carolin 2007) (Fig. 7E). However, anatomical examination of *Velleia* ovary sections by Carolin (1959) revealed the floral parts are in fact fused to the ovary to a degree and the stamens are never fully hypogynous and in many species they appear epigynous (Jeanes 1999) (Fig. 4). Carolin (1977) stated that the flowers, fruits and seeds of *Velleia* are similar to those of various species of *Goodenia* and suggested that the morphology of the ovary was not a "reversion to an almost superior ovary but the vestiges of the former inferior condition are retained". The infrageneric classification of *Velleia*, as currently recognised in the *Flora of Australia*, includes three sections (Carolin 1992g), based on the presence of three sepals (sect. *Velleia*) or five, which are either connate into a tube (sect. *Euthales* (R.Br.) Carolin) or free (sect. *Menoceras* R.Br.). While *Velleia* was supported as monophyletic in molecular analyses, it is placed sister to the remaining species in *Goodenia* Clade C (Gardner et al. 2016a; Jabaily et al. 2018).

Inflorescence structure in *Goodenia* and allied genera

Genera within *Goodenia s.l.* display a wide variation in floral form. Carolin (1967a) suggested the inflorescence structure was based on an open, polytelic, thyrsoid form with bracts that may be leaf-like (Fig. 2H) or reduced. The component axillary cymules of the 'primitive' thyrse may become reduced to form racemes and spikes (Fig. 3A), or the main axis may contract to form subumbels (Carolin et al. 1992) (Fig. 2C). Carolin (1967a) outlined nine reference 'types' that summarise the variation in the "Bauplan" across *Goodenia s.l.* While some inflorescence forms correspond to various infrageneric groups, Carolin's (1967a) survey of inflorescence structure was not comprehensive enough to extrapolate further. Therefore, a more complete survey was undertaken across the Core Goodeniaceae to determine if patterns in floral form are diagnostic and correspond to monophyletic groups recovered in our molecular analyses.

Aims

Roger Carolin's lifetime of work provides a sound framework to test hypotheses about evolutionary relationships in Goodeniaceae and allow for a re-examination of his generic concepts and infrageneric groups. The aim of this study is to build on our previous research (Jabaily et al. 2012; Gardner et al. 2016a; Jabaily et al. 2018) to produce well-sampled and well-resolved phylogenies combining both nrDNA (ITS) and cpDNA (*trnL-F*, *matK*) molecular markers. These updated phylogenies, in conjunction with a survey of inflorescence structure, will clarify our understanding of the systematic importance of these features to characterise subclades within *Goodenia s.l.* The time has now come to also update Carolin's *Flora of Australia* classification to reflect these findings and to formally name and describe monophyletic clades as infrageneric groups in *Goodenia s.l.* in order to ensure nomenclatural stability going forward.

Methods

Taxon sampling

Our study includes over 95% of described species within *Goodenia s.l.* (Suppl. material 1). This paper includes sequences of *trnL-F* and *matK* from Jabaily et al. (2012), *trnL-F*, *matK*, and nrITS samples from Gardner et al. (2016b) with the majority of accessions new to this study. In some instances, multiple accessions of a taxon were included, including some subspecific taxa, to test for monophyly. A number of informal taxa or phrase-named taxa have also been included such as *Goodenia* sp. Dampier Peninsula (B.J. Carter 675) (Western Australian Herbarium 1998-; Council of Heads of Australasian Herbaria 2006-) to test the genetic uniqueness of these taxa and confirm allied species. Initially, a dataset with all taxa was aligned and analysed, but the backbone relationships between Goodenia Clade A, Clade B, and Clade C were unresolved, as expected from our prior work with these loci. Datasets were then created and analysed separately for all taxon sets (A, B, C), following following Jabaily et al. (2012) and Gardner et al. (2016a). Separating the total dataset by clade allowed for more precise alignment across taxa, particularly within *trnL-F*. As the genus *Coopernookia* was confirmed as sister to *Goodenia s.l.* (Gardner et al. 2016a), *Coopernookia polygalacea* (de Vriese) Carolin was used as the outgroup for all three taxon sets; within Clade B and Clade C, two accessions from Clade A (*Goodenia benthamiana* Carolin and *G. tripartita* Carolin) were included as additional outgroups.

Sequencing and Phylogenetic inference

Molecular sequencing primers and protocols follows Gardner et al. (2016a). Sequencing was completed by Macrogen (Seoul, South Korea). Individual loci were aligned in Geneious v. 11.0.2 (Kearse et al. 2012) using the Geneious tree building algorithm, with subsequent manual correction. For all taxon sets (A, B, C), three separate alignments were made for the chloroplast loci (*matK* and *trnL-F*), nuclear ribosomal locus (nrITS), and all data combined (*matK*, *trnL-F*, and nrITS). For each taxon set, individual loci were analysed for models of molecular evolution with Akaike information criterion (AIC) implemented in jModelTest2 (Guindon and Gascuel 2003; Darriba et al. 2012), implemented in CIPRES Science Gateway (Phylo.org; Miller et al. 2010). For the nrITS dataset of Clade B, the model selected was SYM + G + I. For the nrITS and cpDNA datasets of Clade A, the model selected was GTR + G. For the nrITS and cpDNA datasets of Clade C and the cpDNA dataset of Clade B, the model selected was GTR + G +I.

Bayesian phylogenetic analyses using MrBayes 3.2.2 (Ronquist et al. 2012) were conducted in CIPRES Science Gateway. For individual datasets each locus varied independently under the parameters specified by the individual model of molecular evolution. For each Bayesian analysis, two runs were conducted, each with three heated and one cold chain and uniform priors. The heated chain temperature was adjusted to ensure adequate mixing. Each analysis was set to run for up to 100 million generations, autoclosing when the standard deviation of split frequencies reached 0.01. Trees were sampled every 10000 generations, and 25% was discarded as burn-in. The adequacy of each analysis was completed by ensuring effective sample size >100, potential scale reduction factor of ~1.0 for all parameters, and acceptance rates of swaps between adjacent changes was between 0.1–0.7 in Tracer 1.6 (Rambaut et al. 2014). Majority rule consensus trees with posterior probabilities were generated in Geneious.

Maximum likelihood analyses using RAxML v. 8.0 (Stamatakis 2014) were conducted at the high-performance computing cluster (HiPerGator) at the University of Florida using the optimal models of molecular evolution for each dataset as discussed with 1000 bootstrap replications, summarized onto the best ML tree.

Taxonomy and morphology

Typification, synonymy and taxonomy largely follow the *Flora of Australia* treatment (Carolin et al. 1992) and/or the Australian Plant Name Index (https://biodiversity.org.au/nsl/services/APNI). Field work was conducted over several years in southern Western Australia facilitating the collection of fresh samples for DNA sequencing and examination of plants *in situ*. Types and specimens at various herbaria or on loan (AD, BRI, CANB, CGG, DNA, K, LD, MEL, PERTH, W) were also critically examined for the morphological survey of inflorescence structure and for lectotypifications. Further material was viewed using Global Plants (http://plants.jstor.org/) and the Museum National d'Histoire Naturelle online database (https://science.mnhn.fr/institution/mnhn/search) (indicated by "image!" in the citation). Images of seeds of various species were viewed on the Seeds of South Australia website (https://spapps.environment.sa.gov.au/seedsofsa/). Non-Australian species of *Selliera* were assessed using online images available through the *Flora of New Zealand* (http://www.nzflora.info/search.html).

Results

Phylogenetic inference

The cpDNA and nrITS topologies were highly congruent for each taxon set representing Clades A, B and C and no taxon moved between named clades in the nrDNA, cpDNA and combined analyses. For each taxon set, both the chloroplast and nrITS trees (Suppl. materials 2–7) and original alignments (Suppl. materials 8–12) are available. Further, there were no substantial conflicting positions of strongly supported taxa, except where noted below.

Sixty-five accessions were included in the Clade A dataset, representing 50 named taxa (species, subspecies) and four unnamed taxa. Twenty-five of these were not included in previous studies, a 50% increase in taxon coverage. Clade A, representing the majority of species in subsect. *Goodenia*, resolves into two well-supported subclades (Goodenia I and II) with roughly similar numbers of taxa (Fig. 5). The backbone of subclade Goodenia I was poorly supported, with the position of *G. phillipsiae* Carolin (a species previously included in subsect. *Ebracteolatae*) differing between datasets. Similarly, accessions of *Selliera* placed in slightly different subclades. In the nrITS analysis, species of *Selliera* resolve as sister to *G. viscida* (previously included in subg. *Monochila*), several clades removed from *Scaevola collaris* and *G. laevis* Benth.; however, they are placed sister to these species in the cpDNA and combined analyses (Fig. 5). Goodenia II is congruent between datasets and resolves into two subclades. These were congruent between datasets except for a weakly supported subgroup comprising *G. atriplexifolia* A.E.Holland & T.P.Boyle, *G. disperma* F.Muell. and *G. viridula* Carolin that was recovered in the nrITS dataset but not retained in the cpDNA or combined data analyses.

The Clade B dataset comprised 175 accessions of 132 taxa (species, subspecies, and unnamed spp.) including 26 unnamed species. Seventy-seven taxa are newly included in this study, representing 58% of our sampling. Clade B comprises well-supported subclades (Porphyranthus I and II) of sect. *Porphyranthus* that are successively sister to subsect. *Ebracteolatae*, which resolves into strongly supported subclades Ebracteolatae I and II (Figs 6, 7). Taxon composition of these subclades and relative support values are congruent between datasets. In addition to including representatives of Carolin's sect. *Porphyranthus*, the Porphyranthus I clade also comprises two representatives *G. kakadu* Carolin and *G. pumilio* R.Br. from sect. *Amphichila*; a small section of diminutive species found in damp habitats in Northern Australia with the latter species also extending to New Guinea. Our analyses show that *G. chthonocephala* Carolin, a poorly known and unusual cushion-like plant previously included in ser. *Borealis* Carolin, is also allied to these two species (Fig. 6). Further, *G. neogoodenia* Carolin, an atypical species currently included in subsect. *Ebracteolatae*, is allied to another group of northern Australian species in the Porphyranthus I clade. The remaining representatives of Carolin's (1992e) ser. *Borealis* are included in the Ebracteolatae II clade, intermingled with species previously included in ser. *Calogyne* (Fig. 7), while *G. wilunensis* Carolin (subsect. *Goodenia*), is sister to the Ebracteolatae I clade (Fig. 6).

Clade C represents the most morphologically diverse group. Analyses included 92 accessions representing 67 taxa (with 4 being unnamed), a 31% increase in the number of species previously sampled across this clade. Seven individual subclades were well supported: a small group in sect. *Goodenia*, subsections *Scaevolina* and *Coerulea*, subg. *Monochila* and the genera *Velleia*, *Verreauxia* and *Pentaptilon* (Fig. 8). However, the relationships between clades remains unclear. In the combined analysis, subg. *Monochila* and subsect. *Scaevolina* were supported as sister, but this relationship was not found in the individual cpDNA and nrDNA trees. Similarly, *G. xanthotricha* de Vriese and *G. arthrotricha* Benth. were weakly supported as sister to subsect. *Coeruleae* in the combined analysis only. Surprisingly, *G. quadrilocularis* R.Br. is supported as sister to *Velleia* on the nrITS tree while it was sister to the subset of species from subsect. *Goodenia* in the cpDNA and combined analyses.

Inflorescence morphology

Carolin (1967a) originally classified the various inflorescence structures evident in *Goodenia s.l.* into nine different types, based on a relatively limited number of species. A survey of inflorescence morphology across *Goodenia s.l.* was undertaken here, utilising published information, images and herbarium specimens, to confirm key diagnostic characters such as the position and insertion of leaves and bracts, the presence or absence of bracteoles, and overall inflorescence form (Table 2). It should be noted that it is not always easy to distinguish leafy bracts from cauline leaves or between bracts and bracteoles in this group. For example, Albrecht (2002) observed that while *Goodenia halophila* Albr. and *G. cylindrocarpa* Albr. have structures subtending the flowers that look like bracteoles, axillary buds are sometimes present. For that reason, he decided to follow the classification of Briggs and Johnson (1979) and used the term "opposite or sub-opposite bracts" rather than bracteoles. While more accurate in some respects, this terminology is not entirely satisfactory and subsequent authors have continued to use the term bracts for reduced cauline leaves that subtend flowers, and appendages on the flower stalk, when present, are termed bracteoles (Holland and Boyle 2002; Cowie 2005; Pellow and Porter 2005; Sage and Shepherd 2007; Lang 2014). This survey also follows Carolin's concepts for floral structure; however, a more comprehensive evo-devo study of floral development that considers the genetic mechanisms that control branching patterns of the floral-axis (i.e. inflorescences), would greatly improve our understanding of these complex structures.

Carolin's (1967a) original classification of inflorescence structure is now revised to eight different morphologies, characterised as Forms A–H (Fig. 3). Carolin's Type 1 form, seen in the type species *G. ovata* (Fig. 3A), was characterised by the terminal shoot ending with a main inflorescence (MI), subtended by a zone of enrichment (EZ) and then the zone of inhibition or vegetative zone (V) (these labelled HF, BZ and V respectively in Carolin 1967a). The overall structure is a thyrse with leafy bracts, which Carolin observed in other species in subsect. *Goodenia* such as *G. mueckeana* F.Muell.

Table 2. An updated linear sequence and classification for *Goodenia s.l.* including phylogenetic position (NS = species not sequenced) and a summary of morphological characters such as leaf position, inflorescence form and type (as characterised in Figure 2), the presence of leafy (L), bractose (N) or disc-like (D) bracts, and presence (1) or absence (0) of bracteoles. Authorities for most taxa are available in APNI (https://biodiversity.org.au/nsl/services/apni). *Species with an uncertain placement within Clade C.

New linear sequence	Flora of Australia sequence	Current name	Shepherd et al. name	Shepherd et al. classification	Phylogenetic clade	Leaves	Inflorescence form	Inflorescence type	Bracts leafy (L) or bracteose (N)	Bracteoles absent (0); present (1)
1	111	*Goodenia phillipsiae*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_I	cauline	thyrse	A	L	1
2	45	*Goodenia vernicosa*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_I	cauline	raceme; thyrse	A	L	1
3	50	*Goodenia benthamiana*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_I	cauline	raceme	A	L	1
4	43	*Goodenia ovata*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_I	cauline	raceme; thyrse	A	L	1
5	49	*Goodenia amplexans*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_I	cauline	raceme	A	L	1
6	44	*Goodenia varia*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_I	cauline	raceme; thyrse	A	L	1
7	10	*Goodenia viscida*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_I	cauline	spike	A	L	1
8		*Selliera radicans*	*Goodenia radicans*	subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_I	cauline	raceme; solitary	A	L	1
9		*Selliera rotundifolia*	*Goodenia heenanii*	subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_I	cauline	raceme; solitary	A	L	?
10		*Scaevola collaris*	*Goodenia collaris*	subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_I	cauline	raceme; solitary	A	L	1
11	93	*Goodenia laevis* subsp. *laevis*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_I	cauline	raceme; thyrse	A	L	1
12		*Goodenia laevis* subsp. *humifusa*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_I	cauline	raceme; thyrse	A	L	1
13		*Velleia exigua*	*Goodenia exigua*	subg. *Goodenia* sect. *Goodenia*	NS	Basal; cauline	solitary; raceme	A; C	L	1
14		*Goodenia koningsbergeri*		subg. *Goodenia* sect. *Goodenia*	NS	cauline	raceme	A	L	1
15	56	*Goodenia calcarata*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_II	cauline	raceme	A	N, L	1
16	47	*Goodenia chambersii*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_II	cauline	raceme; thyrse	A	L	1

New linear sequence	Flora of Australia sequence	Current name	Shepherd et al. name	Shepherd et al. classification	Phylogenetic clade	Leaves	Inflorescence form	Inflorescence type	Bracts leafy (L) or bracteose (N)	Bracteoles absent (0); present (1)
17		*Goodenia valdentata*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_II	cauline	raceme; thyrse	A	L	1
18	48	*Goodenia kingiana*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_II	cauline	raceme; thyrse	A	L	1
19	53	*Goodenia brunnea*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_II	cauline	raceme; thyrse	A	L	1
20	54	*Goodenia saccata*		subg. *Goodenia* sect. *Goodenia*	NS	cauline	raceme; thyrse	A	L	1
21	46	*Goodenia grandiflora*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_II	cauline	raceme; thyrse	A	L	1
22	51	*Goodenia albiflora*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_II	cauline	raceme	A	L	1
23	57	*Goodenia macmillanii*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_II	cauline	raceme	A	L	1
24	55	*Goodenia stirlingii*		subg. *Goodenia* sect. *Goodenia*	Goodenia ss I_II	cauline	raceme	A	L	1
25	58	*Goodenia fordiana*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal	raceme; solitary	B; C	L	1
26	88	*Goodenia dyeri*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal	solitary	C	L	1
27	83	*Goodenia affinis*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal	raceme; solitary	B; C	L	1
28	86	*Goodenia willisiana*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal	raceme; solitary	B; C	L	1
29	87	*Goodenia robusta*		subg. *Goodenia* sect. *Rosulatae*	NS	basal; cauline	raceme	B	L	1
30	81	*Goodenia geniculata*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal; cauline	raceme; solitary	B; C	L	1
31	82	*Goodenia lanata*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal; cauline	raceme	B	L	1
32	84	*Goodenia convexa*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal	raceme; solitary	B; C	L	1
33	80	*Goodenia blackiana*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal	raceme; solitary	B; C	L	1
34	85	*Goodenia tripartita*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal	raceme; solitary	B; C	L	1
35	90	*Goodenia glabra*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal; cauline	raceme	B	L	1

New linear sequence	Flora of Australia sequence	Current name	Shepherd et al. name	Shepherd et al. classification	Phylogenetic clade	Leaves	Inflorescence form	Inflorescence type	Bracts leafy (L) or bracteose (N)	Bracteoles absent (0); present (1)
36		*Goodenia expansa*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal; cauline	raceme	B	L	1
37	91	*Goodenia peacockiana*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal; cauline	raceme	B	L	1
38	92	*Goodenia schwerinensis*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_I	basal; cauline	raceme	B	L	1
39		*Goodenia atriplexifolia*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_II	cauline	spike	A	L	1
40	68	*Goodenia disperma*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_II	cauline	raceme	A	L	1
41	69	*Goodenia viridula*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_II	cauline	spike	A	L	1
42	70	*Goodenia stephensonii*		subg. *Goodenia* sect. *Rosulatae*	NS	cauline	raceme	A	L	1
43	71a	*Goodenia heterophylla* subsp. *heterophylla*		subg. *Goodenia* sect. *Rosulatae*	NS	cauline	raceme	A	L	1
44	71b	*Goodenia heterophylla* subsp. *egalndulosa*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_II	cauline	raceme	A; B	L	1
45	71c	*Goodenia heterophylla* subsp. *teucriifolia*		subg. *Goodenia* sect. *Rosulatae*	NS	cauline	raceme	A; B	L	1
46	71d	*Goodenia heterophylla* subsp. *montana*		subg. *Goodenia* sect. *Rosulatae*	NS	cauline	raceme	A	L	1
47	72	*Goodenia rotundifolia*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_II	cauline	raceme	A	L	1
48	73	*Goodenia arenicola*		subg. *Goodenia* sect. *Rosulatae*	NS	cauline	solitary	A	?N, L	1
49	76	*Goodenia xanthosperma*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_II	basal; cauline	raceme	B	L	1
50	79	*Goodenia rupestris*		subg. *Goodenia* sect. *Rosulatae*	NS	basal; cauline	raceme	B	L	1
51	94	*Goodenia mueckeana*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_II	basal; cauline	raceme; thyrse	A, B	L	1
52	77	*Goodenia centralis*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_II	basal; cauline	raceme	B	L	1

New linear sequence	Flora of Australia sequence	Current name	Shepherd et al. name	Shepherd et al. classification	Phylogenetic clade	Leaves	Inflorescence form	Inflorescence type	Bracts leafy (L) or bracteose (N)	Bracteoles absent (0); present (1)
53	78	*Goodenia goodeniacea*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_II	basal; cauline	thyrse	B	L	1
54	75	*Goodenia hederacea* subsp. *hederacea*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_II	basal; cauline	raceme; thyrse	B	L	1
55	75a	*Goodenia hederacea* subsp. *alpestris*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_II	basal; cauline	raceme	B	L	1
56	74	*Goodenia delicata*		subg. *Goodenia* sect. *Rosulatae*	Goodenia ss II_II	basal; cauline	raceme	B	L	1
57	153	*Goodenia neogoodenia*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal; cauline	raceme	E; F	N; L	0
58	25	*Goodenia claytoniacea*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal; cauline	raceme; thyrse; panicle-like	B	L	1
59	24	*Goodenia modesta*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal; cauline	thyrse; panicle-like	B	L	1
60	23	*Goodenia lyrata*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal; cauline	raceme	B	L	1
61		*Goodenia halophila*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal; cauline	panicle-like	B, E	L, N	1
62		*Goodenia gypsicola*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal	panicle-like	B, E	L, N	1
63	19	*Goodenia minutiflora*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal	raceme; thyrse	E	N	1

New linear sequence	Flora of Australia sequence	Current name	Shepherd et al. name	Shepherd et al. classification	Phylogenetic clade	Leaves	Inflorescence form	Inflorescence type	Bracts leafy (L) or bracteose (N)	Bracteoles absent (0); present (1)
64	20	*Goodenia viscidula*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal	thyrse; panicle-like	B, E	L, N	1
65	16	*Goodenia bicolor*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal; cauline	raceme; thyrse	E	N	1
66	18	*Goodenia purpurascens*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal	thyrse; panicle-like	E	N	1
67	22	*Goodenia berringbinensis*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal	raceme; thyrse	E	N	1
68	15	*Goodenia lamprosperma*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal; cauline	raceme; thyrse	B	L	1
69		*Goodenia corralina*		subg. *Porphyranthus* sect. *Porphyranthus*	NS	basal; cauline	raceme; thyrse	B, E	L, N	1
70		*Goodenia cylindrocarpa*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal	panicle-like	B, E	L, N	1
71		*Goodenia nocoleche*		subg. *Porphyranthus* sect. *Porphyranthus*	NS	basal; cauline	raceme	B, E	L; N	1
72	165	*Goodenia chthonocephala*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal	solitary	D	L	0
73	178	*Goodenia kakadu*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal; cauline	solitary; raceme	D; F	L	0

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74		*Goodenia oenpelliensis*		subg. *Porphyranthus* sect. *Porphyranthus*	NS	basal; cauline	solitary; raceme	D; F	L	0
75	177	*Goodenia pumilio*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus I	basal; cauline	solitary	D	L	0
76		*Goodenia cravenii*		subg. *Porphyranthus* sect. *Porphyranthus*	NS	basal	solitary; raceme	D; F	L	0
77	17	*Goodenia gloeophylla*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus II	basal; cauline	raceme	B	L	1
78	13	*Goodenia macbarronii*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus II	basal (mostly); cauline	raceme; thyrse	E	N	1
79	12	*Goodenia paniculata*		subg. *Porphyranthus* sect. *Porphyranthus*	NS	basal	raceme; thyrse or panicle-like	B, E	L, N	1
80	14	*Goodenia humilis*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus II	basal	raceme	E	N	1
81	11	*Goodenia gracilis*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus II	basal; cauline	raceme; thyrse	E	N	1
82		*Goodenia rosulata*		subg. *Porphyranthus* sect. *Porphyranthus*	Porphyranthus II	basal; cauline	thyrse; panicle-like	E	N	1
83	89	*Goodenia wilunensis*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme	B	L	1

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84	149	*Goodenia cusackiana*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme	F	N	0
85	139	*Goodenia armitiana*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme; subumbel	F	L	0
86	141	*Goodenia triodiophila*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	cauline	raceme; subumbel	F	L	0
87	143	*Goodenia nuda*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme; subumbel	F	L	0
88	144	*Goodenia pallida*		subg. *Porphyranthus* sect. *Ebracteolatae*	NS	basal; cauline	raceme; subumbel	F	L	0
89	148	*Goodenia tenuiloba*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme	F	L	0
90	150	*Goodenia vilmorinae*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme; subumbel	F	L	0
91	142	*Goodenia microptera*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme; subumbel	F	L	0
92		*Goodenia maretensis*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme; subumbel	F	L	0
93	110	*Goodenia pinnatifida*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme; subumbel	F	L	0
94	120	*Goodenia lobata*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme; subumbel	F	L	0
95	121	*Goodenia salmoniana*		subg. *Porphyranthus* sect. *Ebracteolatae*	NS	?basal; cauline	raceme	F	L	0
96		*Goodenia jaurdiensis*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme	F	L	0

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97	115	*Goodenia mimuloides*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme	F	L	0
98		*Goodenia heatheriana*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme	F	L	0
99	109	*Goodenia pusilliflora*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme	F	L	0
100	107	*Goodenia integerrima*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	subumbel	F	L	0
101		*Goodenia salina*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme; subumbel	F	L	0
102	102	*Goodenia pusilla*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme	F	L	0
103		*Goodenia turleyae*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme	F	L	0
104	123	*Goodenia filiformis*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme; subumbel	F	L	0
105	122	*Goodenia pulchella*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme; subumbel	F	L	0
106	128	*Goodenia micrantha*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme	F	L	0
107	125	*Goodenia quasilibera*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme; subumbel	F	L	0
108	124	*Goodenia concinna*		subg. *Porphyranthus* sect. *Ebracteolatae*	NS	basal	raceme; subumbel	F	L	0
109	126	*Goodenia occidentalis*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme; subumbel	F	L	0

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110	127	*Goodenia krauseana*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	subumbel	F	L	0
111		*Goodenia granitica*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme	F	L	0
112	129	*Goodenia havilandii*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme	F	L	0
113	105	*Goodenia corynocarpa*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme; subumbel	F	L	0
114	114	*Goodenia ochracea*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme	F	L	0
115	113	*Goodenia berardiana*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme; subumbel	F	L	0
116	104	*Goodenia maideniana*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme; subumbel	F	L	0
117	103	*Goodenia anfracta*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme; subumbel	F	L	0
118		*Goodenia pedicellata*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	solitary; raceme	D; F	L	0
119	100	*Goodenia pascua*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme; subumbel	F	L	0
120	101	*Goodenia heteromera*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	subumbel; solitary	F	L	0
121	97	*Goodenia glauca*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme	B; F	L	1; 0
122	98	*Goodenia fascicularis*		subg. *Porphyranthus* sect. *Ebracteolatae*	NS	basal; cauline	raceme; subumbel	F	L	0

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123	108	*Goodenia strangfordii*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	cauline	raceme; subumbel	F	L	0
124	118	*Goodenia megasepala*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme; subumbel	F	L	0
125	99	*Goodenia lunata*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	raceme; subumbel	F	L	0
126		*Goodenia asteriscus*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal	subumbel	F	L	0
127	117	*Goodenia elongata*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae I	basal; cauline	raceme	F	L	0
128	132	*Goodenia heterochila*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	B; F	L	1; 0
129	131	*Goodenia cycloptera*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel	F	L	0
130	112	*Goodenia gibbosa*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel	F	L	0
131	119	*Goodenia iyouta*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme	F	L	0
132	140	*Goodenia virgata*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel	F	L	0
133		*Goodenia effusa*		subg. *Porphyranthus* sect. *Ebracteolatae*	NS	basal; cauline	raceme; subumbel	F	L	0
134	145	*Goodenia prostrata*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal	raceme; subumbel	F	L	0
135	147	*Goodenia forrestii*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme	F	L	0

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136	146	*Goodenia muelleriana*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel	F	L	0
137	116	*Goodenia macroplectra*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel	F	L	0
138	96	*Goodenia angustifolia*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	B, F	L	0, 1
139	95	*Goodenia nigrescens*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	B	L	1
140	133	*Goodenia glandulosa*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme	F	L	0
141	135	*Goodenia faucium*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme	F	L	0
142	134	*Goodenia larapinta*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
143	138	*Goodenia cirrifica*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	B	L	1
144	106	*Goodenia coronopifolia*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal	raceme	F	L	0
145	130	*Goodenia janamba*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal	raceme; subumbel	F	N	0
146		*Goodenia psammophila* subsp. *psammophila*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel	F	L	0
147		*Goodenia psammophila* subsp. *hiddinsiana*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
148	155	*Goodenia arachnoidea*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel	F	L	0

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149		*Goodenia pritzelii*		subg. *Porphyranthus* sect. *Ebracteolatae*	NS	basal; cauline	raceme; subumbel	F	L	0
150	137	*Goodenia odonnellii*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel	F	L	0
151	136	*Goodenia redacta*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel	F	L	0
152	152	*Goodenia stellata*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
153		*Goodenia crenata*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel	F	L	0
154	151	*Goodenia hirsuta*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel	F; B	L	0; 1
155	158	*Goodenia durackiana*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
156	154	*Goodenia sepalosa* var. *sepalosa*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
157	154	*Goodenia sepalosa* var. *glandulosa*		subg. *Porphyranthus* sect. *Ebracteolatae*	NS	basal; cauline	raceme	F	L	0
158	156	*Goodenia brachypoda*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme	F	L	0
159	173	*Goodenia heppleana*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
160	174	*Goodenia symonii*		subg. *Porphyranthus* sect. *Ebracteolatae*	NS	basal; cauline	raceme	F	L	0
161	176	*Goodenia quadrifida*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0

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162	162	*Goodenia potamica*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
163	175	*Goodenia purpurea*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
164	172	*Goodenia holtzeana*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel (rarely)	F	L	0
165	169	*Goodenia pilosa* subsp. *pilosa*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
166		*Goodenia pilosa* subsp. *chinensis*		subg. *Porphyranthus* sect. *Ebracteolatae*	NS	basal; cauline	raceme	F	L	0
167	168	*Goodenia porphyrea*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme	F	L	0
168	170	*Goodenia neglecta*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme; subumbel	F	L	0
169		*Goodenia inundata*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme; subumbel	F	L	0
170	166	*Goodenia armstrongiana*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme	F	L	0
171		*Goodenia debilis*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
172		*Goodenia elaiosoma*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme	F	L	0
173		*Goodenia heterotricha*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme; thyrse	F	L	0
174	164	*Goodenia subauriculata*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme	F	L	0

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175	160	*Goodenia campestris*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
176	159	*Goodenia byrnesii*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
177	167	*Goodenia argillacea*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme	F	L	0
178	161	*Goodenia malvina*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	cauline	raceme	F	L	0
179	157	*Goodenia leiosperma*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
180	163	*Goodenia hispida*		subg. *Porphyranthus* sect. *Ebracteolatae*	Ebracteolatae II	basal; cauline	raceme	F	L	0
181	34	*Goodenia coerulea*		subg. *Monochila* sect. *Coeruleae*	Coerulea	basal; cauline	raceme; thyrse	E	N	1
182	37	*Goodenia incana*		subg. *Monochila* sect. *Coeruleae*	Coerulea	basal; cauline	raceme	B	L	1
183	39	*Goodenia glareicola*		subg. *Monochila* sect. *Coeruleae*	Coerulea	basal	raceme; panicle-like	E	N	1
184	35	*Goodenia trichophylla*		subg. *Monochila* sect. *Coeruleae*	Coerulea	basal; cauline	raceme; thyrse	E	N	1
185	36	*Goodenia perryi*		subg. *Monochila* sect. *Coeruleae*	Coerulea	basal; cauline	raceme	E	N	1
186	38	*Goodenia pterigosperma*		subg. *Monochila* sect. *Coeruleae*	Coerulea	basal; cauline	raceme; thyrse	E	N	1
187	40	*Goodenia eatoniana*		subg. *Monochila* sect. *Coeruleae*	Coerulea	basal; cauline	raceme; thyrse	E	L	1
188	42	*Goodenia hassallii*		subg. *Monochila* sect. *Coeruleae*	Coerulea	basal; cauline	raceme; thyrse	E	L	1
189		*Goodenia katabudjar*		subg. *Monochila* sect. *Coeruleae*	Coerulea	basal; cauline	raceme	E	L	1
190	41	*Goodenia leptoclada*		subg. *Monochila* sect. *Coeruleae*	NS	basal; cauline	raceme	E	L	1

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191		*Goodenia lancifolia*		subg. *Monochila* sect. *Coeruleae*	NS	basal; cauline	raceme	E	L	1
192	59	*Goodenia quadrilocularis*		subg. *Monochila* sect. *Tetraphylax*	Tetrathylax	basal; cauline	raceme	E	N	1
193	65	*Goodenia lineata*		subg. *Monochila* sect. *Tetraphylax*	Tetrathylax	basal	raceme (panicle?)	E	N	1
194	67a	*Goodenia racemosa* var. *racemosa*		subg. *Monochila* sect. *Tetraphylax*	Tetrathylax	cauline	raceme; thyrse	G	N	1
195	67b	*Goodenia racemosa* var. *latifolia*		subg. *Monochila* sect. *Tetraphylax*	NS	cauline	raceme; thyrse	G	N	1
196	64	*Goodenia glomerata*		subg. *Monochila* sect. *Tetraphylax*	Tetrathylax	basal; cauline	spike	E	N	1
197	62a	*Goodenia dimorpha* var. *dimorpha*		subg. *Monochila* sect. *Tetraphylax*	NS	basal; cauline	thyrse-like panicle	E	N	1
198	62b	*Goodenia dimorpha* var. *angustifolia*		subg. *Monochila* sect. *Tetraphylax*	Tetrathylax	basal; cauline	thyrse-like panicle	E	N	1
199	63	*Goodenia stelligera*		subg. *Monochila* sect. *Tetraphylax*	Tetrathylax	basal; cauline	raceme; thyrse	E	N	1
200	66a	*Goodenia bellidifolia* subsp. *bellidifolia*		subg. *Monochila* sect. *Tetraphylax*	Tetrathylax	basal	raceme	E	N	1
201	66b	*Goodenia bellidifolia* subsp. *argentea*		subg. *Monochila* sect. *Tetraphylax*	NS	basal; cauline	raceme	E	N	1
202	60	*Goodenia decurrens*		subg. *Monochila* sect. *Tetraphylax*	Tetrathylax	basal (indeterminate); cauline	raceme; thyrse	G	N	1
203	61	*Goodenia rostrivalvis*		subg. *Monochila* sect. *Tetraphylax*	NS	basal	raceme; thyrse	E	N	1
204		*Pentaptilon careyi*	*Goodenia careyi*	subg. *Monochila* sect. *Verreauxia*	Verreauxia	basal; cauline	thyrse	E	N	1
205		*Verreauxia verreauxii*	*Goodenia verreauxii*	subg. *Monochila* sect. *Verreauxia*	Verreauxia	basal	raceme; thyrse	E	N	1
206		*Verreauxia reinwardtii*	*Goodenia reinwardtii*	subg. *Monochila* sect. *Verreauxia*	Verreauxia	cauline	raceme; spike-like thyrse	G	N	1
207		*Verreauxia dyeri*	*Goodenia etheira*	subg. *Monochila* sect. *Verreauxia*	Verreauxia	cauline	raceme; spike-like thyrse	G	N	1

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208	4	*Goodenia pinifolia*		subg. *Monochila* sect. *Monochila* subsect. *Monochila*	Monochila	cauline	raceme; thyrse	G	N	1
209	5	*Goodenia elderi*		subg. *Monochila* sect. *Monochila* subsect. *Monochila*	Monochila	cauline	raceme; thyrse	G	N	1
210	26	*Goodenia sericostachya*		subg. *Monochila* sect. *Monochila* subsect. *Monochila*	Monochila	basal; cauline	spike	G	N	1
211		*Goodenia scapigera* subsp. *graniticola*		subg. *Monochila* sect. *Monochila* subsect. *Monochila*	Monochila	cauline	raceme; thyrse	G	L	1
212	1	*Goodenia scapigera* subsp. *scapigera*		subg. *Monochila* sect. *Monochila* subsect. *Monochila*	Monochila	cauline	thyrse	G	N	1
213	3a	*Goodenia watsonii* subsp. *watsonii*		subg. *Monochila* sect. *Monochila* subsect. *Monochila*	NS	basal	thyrse	E	N	1
214	3b	*Goodenia watsonii* subsp. *glandulosa*		subg. *Monochila* sect. *Monochila* subsect. *Monochila*	Monochila	basal	thyrse	E	N	1
215	2	*Goodenia decursiva*		subg. *Monochila* sect. *Monochila* subsect. *Monochila*	Monochila	cauline	thyrse	G	N	1
216	7	*Goodenia stenophylla*		subg. *Monochila* sect. *Monochila* subsect. *Infracta*	Monochila	cauline	spike; spike like thyrse	G	N	1
217	8	*Goodenia drummondii* subsp. *drummondii*		subg. *Monochila* sect. *Monochila* subsect. *Infracta*	Monochila	cauline	spike; spike-like thyrse	G	N	1

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218		*Goodenia drummondii* subsp. *megaphylla*		subg. *Monochila* sect. *Monochila* subsect. *Infracta*	NS	cauline	spike; spike-like thyrse	G	N	1
219	9	*Goodenia helmsii*		subg. *Monochila* sect. *Monochila* subsect. *Infracta*	Monochila	cauline	spike; spike-like thyrse	G	N	1
220	6	*Goodenia fasciculata*		subg. *Monochila* sect. *Monochila* subsect. *Infracta*	Monochila	cauline	spike; spike-like thyrse	G	N	1
221		*Goodenia hartiana*		subg. *Monochila* sect. *Scaevolina*	Scaevolina	cauline	raceme	B	L	1
222	27	*Goodenia scaevolina*		subg. *Monochila* sect. *Scaevolina*	Scaevolina	basal; cauline	raceme; thyrse	B	L	1
223	28	*Goodenia stobbsiana*		subg. *Monochila* sect. *Scaevolina*	Scaevolina	basal; cauline	thyrse	B	L	1
224	33	*Goodenia azurea* subsp. *azurea*		subg. *Monochila* sect. *Scaevolina*	Scaevolina	cauline	raceme; thyrse	B	L	1
225		*Goodenia azurea* subsp. *hesperia*		subg. *Monochila* sect. *Scaevolina*	Scaevolina	cauline	raceme; thyrse	B	L	1
226	29	*Goodenia suffrutescens*		subg. *Monochila* sect. *Scaevolina*	Scaevolina	cauline	thyrse	B	L	1
227		*Goodenia splendida*		subg. *Monochila* sect. *Scaevolina*	Scaevolina	cauline	raceme	B	L	1
228	32	*Goodenia ramelii*		subg. *Monochila* sect. *Scaevolina*	Scaevolina	basal; cauline	raceme; thyrse	E	N	1
229	31	*Goodenia eremophila*		subg. *Monochila* sect. *Scaevolina*	Scaevolina	basal; cauline	thyrse	B	L	1
230	2	*Velleia foliosa*	*Goodenia brendannarum*	subg. *Monochila* sect. *Velleia*	Velleia	basal; cauline	axillary dichasia	H	N	1
231	3	*Velleia macrophylla*	*Goodenia macrophylla*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	N	1
232	1	*Velleia trinervis*	*Goodenia trinervis*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	N, L	1
233	14	*Velleia glabrata*	*Goodenia glabrata*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	N, L	1
234	11	*Velleia hispida*	*Goodenia capillosa*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	N, L	1
235	13	*Velleia paradoxa*	*Goodenia paradoxa*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	N	1

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236	10	*Velleia cycnopotamica*	*Goodenia cycnopotamica*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	N	1
237	9	*Velleia rosea*	*Goodenia rosea*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	N	1
238	12	*Velleia arguta*	*Goodenia arguta*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	N	1
239	8	*Velleia discophora*	*Goodenia discophora*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	D	1
240	6	*Velleia panduriformis*	*Goodenia panduriformis*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	D	1
241	7	*Velleia connata*	*Goodenia connata*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	D	1
242	5	*Velleia daviesii*	*Goodenia daviesii*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	L	1
243	19	*Velleia macrocalyx*	*Goodenia macrocalyx*	subg. *Monochila* sect. *Velleia*	Velleia	basal; cauline	axillary dichasia	H	N	1
244	20	*Velleia perfoliata*	*Goodenia perfoliata*	subg. *Monochila* sect. *Velleia*	NS	basal	axillary dichasia	H	D	1
245	21	*Velleia montana*	*Goodenia montana*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	N	1
246	15	*Velleia lyrata*	*Goodenia caroliniana*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	N	1
247	16	*Velleia parvisepta*	*Goodenia parvisepta*	subg. *Monochila* sect. *Velleia*	NS	basal	axillary dichasia	H	N	1
248	18	*Velleia pubescens*	*Goodenia subsolana*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	N	1
249	17	*Velleia spathulata*	*Goodenia mystrophylla*	subg. *Monochila* sect. *Velleia*	Velleia	basal	axillary dichasia	H	N	1
250*	30	*Goodenia arthrotricha*		subg. *Monochila*	Clade C (unplaced)	basal; cauline	raceme; thyrse	B	L	1
251*	52	*Goodenia xanthotricha*		subg. *Monochila*	Clade C (unplaced)	cauline	raceme	B	L	1

(see table 1 in Carolin 1967a, note the infrageneric classification in that work follows Krause 1912). The subsequent year's growth in this inflorescence type is continued by lateral buds in the inhibition zone of the previous year's growth. In Carolin's Type 2 form, every partial inflorescence is reduced to 1(–2) flower(s) per raceme, as observed in species of *Coopernookia* and other members of subsect. *Goodenia* such as *G. laevis* (Fig. 3A inset) and *G. calcarata* (F.Muell.) F.Muell. Type 1 and 2 inflorescence forms intergrade somewhat, as some species such as *G. varia* R.Br. and *G. grandiflora* Sims were recorded by Carolin (1967a) as having both a Type 1 and Type 2 Bauplan. As such, these two inflorescence types have been combined into a new category designated as Form A. This form occurs in all species in the Goodenia I subclade of Clade A, and several species allied to *G. atriplexfolia* in the Goodenia II subclade (Table 2). Other species in this latter clade also exhibit inflorescence Form B previously known as Carolin's Type 5, which have a basal rosette but with leafy bracteoles, as observed in *G. hederacea* Sm. (Fig. 3B) and species allied to *G. affinis* de Vriese in subsect. *Goodenia*. A small group in this category from subg. *Porphyranthus* may have inflorescences that are panicle-like; however, some of the lateral inflorescences from the main stem appear to be monochasial cymes, where the youngest flowers emerge from the axil of a bract below older flowers or may be reduced to a single flower (D. Albrecht pers. comm.). Carolin (1967a) noted that *G. rotundifolia* R.Br. exhibited a Type 5 inflorescence (see table 1, Carolin 1967a), but this species tends to have cauline leaves and leafy racemes rather than a basal rosette, so its inflorescence is correctly categorised as Form A. Carolin also observed that among *G. hederacea* and allied species the main stem may not produce an inflorescence in a given year, presumably due to poor growing conditions, continuing with vegetative growth potentially for several years, as the inflorescences are entirely a product of the enrichment zone.

Two inflorescence groups that were previously not characterised by Carolin are recognised here. A number of small, tufted herbaceous species in the Goodenia II subclade allied to *G. convexa* Carolin show a reduction of the inhibition zone and the vegetative branching zone to form a basal rosette of leaves, but with solitary, bracteolate flowers produced in the axils of the basal leaves. These species are categorised as having a Form C inflorescence (Fig. 3C). While another group of herbs from the Porphyranthus I clade including the diminutive *G. chthonocephala* Carolin, as well as *G. kakadu* and *G. pumilio* previously included in sect. *Amphichila* along with the recently described *G. cravenii* (Fig. 6C) and *G. oenpelliensis* R.L.Barrett, all have ebracteolate, solitary flowers in leaf axils, which is categorised here as Form D (Fig. 3D). It should be noted that *G. oenpelliensis*, which is currently only known from a single locality in the Northern Territory, has dimorphic inflorescences with both solitary flowers and short, ebracteolate cymes (Barrett and Barrett 2018), the latter type being categorised as Form F (see below and Fig. 3F).

Species characterised as having a Form E inflorescence herein include a diverse group from the Porphyranthus subclades of Clade B and representatives of the Coreulea, Tetrathylax, Verreauxia and Scaevolina subclades of Clade C that have a basal rosette of leaves and inflorescences with non-leafy bracts and bracteoles that form panicles (e.g. *G. paniculata* Sm., Fig. 3E), racemes (e.g. *G. gracilis* R.Br., Fig. 3E inset above), or a thyrse-like inflorescence (e.g. *G. pterygosperma* Krause, Fig. 3E inset below).

Species of *Goodenia* lacking bracteoles from subsects. *Ebracteolatae* and *Borealis* currently placed in the Ebraceolatae subclades of Clade B were variously categorised under Carolin's inflorescence Types 6–8. Carolin's Type 6 inflorescence morphology was characterised by leafy, ebracteolate racemes, as observed in various species in subsect. *Ebracteolatae* such as *G. hispida* R.Br. (Fig. 3F). Previously, *G. pumilio*, from sect. *Amphichila*, was also recorded as having a Type 6 inflorescence but as stated above, this morphology is now treated as Form D. Carolin's Type 7 group included species with an inflorescence similar in form to Type 6 but with reduced, non-leafy bracts (e.g. *G. pinnatifida* Schltdl., *G. fascicularis* F.Muell. & Tate (Fig. 3F inset above), and allied species). Carolin (1967a) noted that *G. cycloptera* R.Br. had both Type 6 and Type 7 inflorescences, while *G. filiformis* R.Br., also from subsect. *Ebracteolatae*, was documented as having both Type 7 and Type 8 inflorescences, the latter form characterised by an inflorescence where the internodes are shortened to form a subumbel and the bracts are leaf-like, as observed in *G. concinna* Benth. (Fig. 2C) and *G. pulchella* Benth. (Fig. 3F inset below). It is now evident that many species in the Ebraceolatae subclades of Clade B may exhibit variations in inflorescence morphology, particularly when growing under varying seasonal conditions, and so Carolin's inflorescence Types 6–8 are grouped together here under Form F (Table 2).

Carolin's Type 3 inflorescence (here treated as Form G) was defined as being the same as Type 1 but the bracteoles are reduced rather than leafy. This was observed in members of subg. *Monochila*, for example *G. scapigera* R.Br. (Figs 2G, 3G) and *G. racemosa* F.Muell., as well as *Verreauxia reinwardtii* (de Vriese) Benth.

Finally, Carolin (1967a) treated species in the genus *Velleia* as having a Bauplan that was a modification of the Type 1 form (recognised here as Form H), where the whole of the terminal "paracladium" (the enrichment zone) is contracted and the inflorescences are elongated with each partial inflorescence expanding into complex branching dichasia or "dichotomous axillary cymes" forming a significant component of the overall plant habit (Carolin 1967c). Carolin (1967a) also noted that the terminal bud apparently continues to grow from year to year.

Discussion

Taxonomic stability is important, particularly in species-rich groups that are horticulturally popular such as the family Goodeniaceae. Under-sampling in phylogenetic studies can result in premature taxonomic decisions as the addition of further taxa or more informative data may highlight significant incongruencies. This is often most problematic in groups with poor backbone resolution. In light of this, we have been reluctant to make taxonomic changes based on our previous molecular phylogenetic studies, particularly within the morphologically diverse *Goodenia s.l.* (Jabaily et al. 2012; Gardner et al. 2016a; Jabaily et al. 2018). Through ongoing studies, we now believe we have addressed key sampling and data issues by including multiple accessions and combining genome skimming and Sanger sequencing from across multiple gene regions and genomic compartments. A number of potentially new phrase-named species (designated by 'sp.' and a relevant phrase name e.g. *Goodenia* sp. Mount Bomford (M.D. Barrett 423)) that are currently recognised on Australian plant name databases (Council of Heads of Australasian Herbaria, 2006-; Western Australian Herbarium, 1998-), and variants that show an affinity to but may be distinct from current species ('aff'), were also included in this study. Australia has a high level of species discovery and description (Wege et al. 2015), and yet many taxa that have been provisionally recognised as new are yet to be formally named and described. Western Australia is a centre for diversity for many groups including *Goodenia* with more than 70% of known species of this genus found there. Given that approximately 44% of the state's undescribed taxa are listed as being poorly known and of conservation concern (Smith and Jones 2018), with many facing continued significant threat due to land clearing and habitat fragmentation, fire, weed invasion, disease and climate change, it is essential that the description of new taxa is expedited. By including variants and phrase-named taxa in molecular phylogenies, their closest allied taxa can be confirmed, thus focusing taxonomic study to the most relevant species group to facilitate their taxonomic resolution.

The results of this molecular study reconfirm our earlier findings where *Goodenia s.l.* is paraphyletic with respect to *Pentaptilon*, *Selliera*, *Velleia*, and *Verreauxia* (Jabaily et al. 2012; Gardner et al. 2016a; Jabaily et al. 2018). Unfortunately, there are no obvious synapomorphies that define this broad group and yet the various included genera are relatively morphologically well circumscribed. This led to earlier suggestions that *Goodenia* could potentially be more narrowly defined to represent only the species within Clade A (including *Selliera* and *Scaevola collaris*), as the newly conserved type *G. ovata* (Shepherd et al. 2017) falls within this clade. In this case, *Pentaptilon*, *Velleia* and *Verreauxia* would be retained along with several newly reinstated or circumscribed segregate genera. However, this outcome would be significantly more taxonomically disruptive as around 160 name changes would be required, mostly in the species-rich Clade B where the earliest available name is *Calogyne*. Moreover, phylogenetic under-resolution and conflict remains within floristically diverse Clade C, likely due to recent radiation, possible hybridisation and incomplete lineage sorting. This, in conjunction with our re-assessment of key morphological characters including inflorescence form and ovary structure, and expanded molecular phylogenetic data, has led us to the pragmatic taxonomic decision to synonymise *Pentaptilon*, *Selliera*, *Velleia*, and *Verreauxia* into an expanded *Goodenia*.

Synonymisation of *Diaspasis*

Scaevola is not discussed in detail in this study other than to provide the new combination for the monotypic Western Australian genus *Diaspasis* (Jabaily et al. 2012). *Diaspasis* was first recognised as distinct by Robert Brown (1810) due to its nearly actinomorphic flowers (see Fig. 1E in Jabaily et al. 2012) and connate anthers. *Scaevola* by contrast, typically has fan-like flowers with free anthers (Carolin et al. 1992); however, shared characters between these genera include a dry indehiscent fruit with a hard endocarp and a spathulate embryo (cf. terete in the LAD clade *sensu* Jabaily et al. 2012) and similar trichomes (Carolin 1971). Moreover, Carolin (1959) noted that *D. filifolia* had a similar anatomical floral and stylar structure to *Scaevola albida* (Sm.) Druce and *S. hookeri* (de Vriese) F.Muell. ex Hook.f. Recent floral morphometric analyses of the Core Goodeniaceae have shown that floral symmetry is quite labile across the family with various species of *Scaevola* tending towards a pseudo-radial symmetry (e.g. *S. phlebopetala* F.Muell.: see Gardner et al. 2016b) somewhat like the form of *D. filifolia*. Molecular data also supports *Diaspasis* as congeneric with *Scaevola* (Howarth et al. 2003; Jabaily et al. 2012; Gardner et al. 2016a) and so a new combination for this species is provided.

No synapomorphic characters define *Goodenia s.l.*

Key characters previously used to distinguish *Goodenia* (Carolin 1992e) include bilabiate flowers, an inferior ovary that has 2 incomplete locules with > 2 ovules either present in two rows or scattered over the surface of the placenta, and fruits being dry, bi-valved, dehiscent capsules with flat seeds that have a rim or wing (Fig. 2F). Carolin (1992e) did note there were exceptions, such as *G. neogoodenia* and some representatives of the fan-flowered subg. *Monochila*, which have 1-seeded, indehiscent nuts, as does the newly included *Scaevola collaris* (Fig. 2B). Moreover, molecular sequence data show that species of *Selliera* that have indehiscent dry or fleshy fruits are also embedded within *Goodenia.* Clearly these various indehiscent fruits are superficially similar, but evidently non-homologous, to the indehiscent fruits of *Scaevola*; a diagnostic character for that genus. Further, the fan-flower form typical for *Scaevola* has also evolved independently across every major clade in *Goodenia* (Gardner et al. 2016b). It was evident to Carolin (1966) that while *Scaevola* and *Goodenia* were allied, these genera had distinct evolutionary histories and that the "similarities in the ovary structure are the result of convergence rather than common origin" as the locules in the ovary of *Goodenia* are derived from two carpels rather than one as evident in *Scaevola* (Carolin 1959). While there are no easily discernible synapomorphies available for *Goodenia s.l.*, this is a well-supported clade, so a combination of characters is required to recircumscribe this genus. Thus, a revised classification based on our understanding of phylogenetic relationships within the newly expanded *Goodenia* is outlined, recognising monophyletic groups at infrageneric levels (Table 1) including three newly circumscribed subgenera *Goodenia*, *Porphyranthus* and *Monochila* representing Clades A, B and C respectively.

New infrageneric taxa within subgenus *Goodenia* (Goodenia Clade A)

Subgenus *Goodenia* as recognised herein reflects Carolin's (1992e) subsect. *Goodenia* in most respects, with two major clades (Goodenia I and Goodenia II) now formally recognised as sections (Table 1). Goodenia I includes the newly conserved type species

G. ovata (Shepherd et al. 2017) and so represents sect. *Goodenia*, while Goodenia II is a recircumscription of Krause's (1912) ser. *Rosulatae* K.Krause, recognised herein as sect. *Rosulatae* (K.Krause) K.A.Sheph.

In the combined molecular analysis, Goodenia I includes *G. phillipsiae*; a species previously placed in sect. *Ebracteolatae* despite the presence of bracteoles, although Carolin (1992e) did acknowledge that this was a species of "uncertain affinity" as apparent related species were ebracteolate. The typical subclade with *G. ovata* and allied species includes prostrate or decumbent subshrubs, many of which have long stoloniferous branches that may root at the nodes (Fig. 2I). These plants are usually glabrous or viscid, with bright yellow bilabiate flowers where the dorsal lobes are erect and sometimes overlapping (Fig. 5A, E–G). One exception is *G. viscida* (Fig. 5C), an erect fan-flowered subshrub from south-west Western Australia. Carolin et al. (1992) was also uncertain of the systematic placement of this species but included it in subg. *Monochila* due its yellow fan-shaped flowers, despite the fact *G. viscida* "has a seed-surface pattern unlike any other species [within the subgenus] and is therefore likely to be misplaced" (Carolin 1980).

The second subclade in Goodenia I includes *Selliera*, a small genus of prostrate, woody perennials with white or pale pink fan-flowers that have fleshy fruits that become woody and corky with age, which are found near coastal, winter-wet or saline flats (Fig. 5B) in Australia, New Zealand and Chile. Also in this clade is *Scaevola collaris* (Fig. 2C), a widespread fan-flowered species often found around the margins of salt lakes across arid Australia with a uniquely beaked fruit with a sponge-like woody endocarp. This unusual species is placed sister to *G. laevis*, which is confined to the southern regions of Western Australia and has capsular fruits as seen in the rest of sect. *Goodenia*. However, in a surprising twist, recent analysis of new ITS sequence data has shown that the enigmatic species *Velleia exigua* (F.Muell.) Carolin is in fact more closely allied to *G. laevis* (R. Jabaily, unpublished data). Initial attempts to molecular sequence *V. exigua* had failed, and its systematic position was equivocal. This species was previously included in *Goodenia* (as *G. exigua* F.Muell.) and while Carolin (1992g) transferred it to *Velleia* sect. *Euthales*, he noted that it was unlike other species of the genus due to the presence of solitary and almost sessile flowers, and sepals that were adnate to the ovary in the lower half (in contrast to all other species where the sepals are adnate to the base of the ovary). The indusium of *V. exigua* was also considered to be unique within *Velleia*, but on close inspection it is remarkably similar to that seen in *Goodenia viscida* and indeed *Scaevola collaris*, which was described by Carolin (1992g) as being obloid and longer than it is wide. Moreover, the indusium in these species is notched at the apex and has no obvious fringing hairs on the lips (Fig. 5C), although tiny hairs are present on the indusium of *S. collaris*. Based on morphological and molecular evidence, it is now clear that *V. exigua* should be included in sect. *Goodenia*.

The final subclade recovered in the Goodenia I clade includes several erect, glabrous subshrubs allied to *G. kingiana* Carolin, that have articulated pedicels and large bilabiate flowers where the dorsal petals are spreading to expose a long style supporting a broad indusium. The South Australian species *G. saccata* Carolin was not sequenced, but it is morphologically allied to *G. grandiflora* Sims and so is included in the typical section.

The Goodenia II subclade, treated here as sect. *Rosulatae* (K.Krause) K.A.Sheph., includes erect or decumbent shrubs and herbs with rosulate and/or cauline leaves that are often covered in a dense tomentum of soft, multicellular hairs. Some species such as *G. rotundifolia* are variable and may be glabrous or have a mix of simple, glandular and multicellular hairs. There are two well supported subclades in this section that are not taxonomically recognised. In the first, *G. fordiana* Carolin is placed sister to a subclade of small tufted herbs from southern Australia allied to *G. convexa*. These species have cottony, multicellular hairs and solitary flowers that are sometimes supported by a distinctly geniculate pedicel that is sharply bent at the point of bracteole attachment. Sister to this, is a less well-resolved group allied to the widespread *G. glabra* R.Br. that includes decumbent herbs or subshrubs from northern and central Australia, which may also have a geniculate pedicel. The second monophyletic group in the Goodenia II subclade includes decumbent plants that occur in more arid inland regions of Australia with a centre of diversity in Queensland. Two potentially new species informally known as *G.* sp. Carnarvon Range (D.J. Edinger Nats 30) and *G.* sp. Mt Castletower (M.D. Crisp 2753) (Council of Heads of Australasian Herbaria 2006-), also fall within this clade. Finally, *G. arenicola* Carolin, a species currently only known from the type locality on Stradbroke Island in Queensland, as well as *G. robusta* (Benth.) K.Krause and *G. rupestris* Carolin, were not successfully sequenced, but are included in sect. *Rosulatae* as they share key diagnostic characters such as low prostrate habit and a tomentum of multicellular hairs. According to Carolin (1992e), *G. stephensonii* F.Muell. is allied to *G. heterophylla* Sm. and this species is placed in sect. *Rosulatae* for now; however, *G. stephensonii* is glandular hairy and somewhat viscid, features that are common to species included in sect. *Goodenia.*

Goodenia wilunensis, *G. xanthotricha*, and a group of species allied to *G. quadrilocularis* were all previously included in Carolin's (1992e) subsect. *Goodenia*, but based on molecular and morphological data these species are now excluded from our recircumscribed subg. *Goodenia* and will be discussed in later sections.

Recognition of *Porphyranthus* as a new subgenus (Goodenia Clade B)

Section *Porphyranthus* is elevated to subgeneric rank herein as subgen. *Porphyranthus* (G.Don) K.A.Sheph., which encompasses the variation evident across the monophyletic Clade B. Two sections corresponding to the two major subclades within this new subgenus are also recognised. G.Don's (1834) original sect. *Porphyranthus*, represented by Porphyranthus I and II in the molecular analyses, is expanded to include sect. *Amphichila*. While Krause's (1912) subsect. *Ebracteolatae*, encompassing the Ebracteolatae I and II clades, is recircumscribed to include both ser. *Borealis* and *Calogyne* of sect. *Borealis* and elevated to a section, recognised here as sect. *Ebracteolatae* (K.Krause) K.A.Sheph. (Table 1).

The reinstatement of *G. rosulata* Domin and recognition of a further three new species (Albrecht 2002; Holland and Boyle 2002; Pellow and Porter 2005; Sage and

Shepherd 2007) in sect. *Porphyranthus* in recent decades has resulted in the expansion of this section from Carolin's (1992e) concept. The majority of species in this group are herbaceous annuals or perennials that grow in sandy soils and winter wet situations and creek beds in eastern and northern Australia, with *G. purpurascens* R.Br. also found in New Guinea (Carolin 1992e). These species generally have basal leaves and spreading, bracteolate inflorescences that may comprise a large part of the plant, and glossy, round seeds that are small (less 1 mm wide) with a very narrow mucilaginous wing c. 0.1 mm wide. *Goodenia kakadu*, *G. pumilio* and the recently described *G. cravenii* (Fig. 6C) and *G. oenpelliensis* (Barrett and Barrett 2014, 2018), are currently included in sect. *Amphichila*. These small, sometimes mat-like herbs have tiny reddish-purple fan-like flowers and small convex seeds with a minute wing. All four species are here transferred to sect. *Porphyranthus* along with *G. chthonocephala*, a species previously included in ser. *Borealis* that has an unusual cushion-like habit and tiny flowers held in a dense head at ground level. The Western Australian *G. neogoodenia*, originally recognised as the monotypic *Neogoodenia minutiflora* due to its tiny wingless corolla, and enlarged, indehiscent, 1-celled fruit (Gardner and George 1963), was transferred by Carolin (1990) to *Goodenia* (in subsect. *Ebracteolatae*). On molecular evidence it is clear *G. neogoodenia* is allied to a group of species in sect. *Porphyranthus* that are often associated with the margins of inland salt lakes including *G. halophila* and *G. gypsicola* Symon (Fig. 2H).

A potentially new Western Australia species, *G.* sp. Mount Bomford (M.D. Barrett 423), placed sister to the purple-flowered *G. gloeophylla* Carolin. Similarly, *G.* sp. Dampier Peninsula (B.J. Carter 675) is shown to be allied to a group that may exhibit an aquatic phase when growing under flooded conditions producing distinctive floating leaves with long petioles as observed in *G. lamprosperma* F.Muell. (Carolin 1992e) and *G. berringbinensis* Carolin (Gibson 2014). *Goodenia nocoleche* Pellow & J.L.Porter, *G. paludicola* Carolin, *G. paniculata* and *G. corralina* L.W.Sage & K.A.Sheph. were not sequenced; however, they are here included in sect. *Porphyranthus* due to the shared presence of a floriferous inflorescence, leafy bracts, bracteoles, and small seeds, with *G. nocoleche* also recorded as producing aquatic leaves under flood conditions (Pellow and Porter 2005).

Over the last two decades, 10 new species have been recognised in Carolin's (1992e) subsect. *Ebracteolatae* (Sage 2000; Sage 2001; Sage and Dixon 2005; Sage and Shepherd 2007; Barrett and Barrett 2014; Barrett and Barrett 2018). This is currently the largest infrageneric group in *Goodenia* and is characterised by a lack of bracteoles, generally yellow flowers, and distinctively winged seeds. Many species are annuals or herbaceous perennials found in the more arid regions of the Australian continent. Indeed, it is evident that the Eremaean interior has been an important source and sink for diversification within this group (Jabaily et al. 2014). In these arid regions, many species are confined to damp areas around the margins of creeks and lakes that germinate or regenerate from rootstock after significant cyclonic rainfall (Sage and Pigott 2003), thus 'avoiding' harsher seasonal conditions during the long dry season. Of interest is the Western Australian bracteolate *G. wilunensis* that placed sister to the Ebracteolatae clade. While this section is characterised as generally being ebracteolate, there are a few other species within this clade that do retain this character, such as *G. nigrescens* Carolin and *G. cirrifica* F.Muell.

As stated, sect. *Ebracteolatae* as recognised here, is expanded to include the former ser. *Borealis* and *Calogyne* of subsect. *Borealis*, a group characterised by leafy inflorescences, a lack of bracteoles and seeds with a prominent rim rather than an obvious wing. Since the *Flora of Australia* treatment (Carolin 1992e), three new species, *G. inundata* L.W.Sage & J.P.Piggot, *G. debilis* A.E.Holland & T.P.Boyle and *G. elaiosoma* Cowie, have been included in ser. *Borealis* (Sage 2001; Holland and Boyle 2002; Cowie 2005), a group segregated on the presence of a simple style and broad sepals to 2.5 mm wide, in contrast to the divided style and narrow sepals to 0.4 mm wide that distinguished ser. *Calogyne*. Species in this former subsection are found in northern Australia, with the exception of *G. armstrongiana* de Vriese (ser. *Borealis*), which also occurs in New Guinea, while the widespread and variable *G. pilosa* (R.Br.) Carolin (ser. *Calogyne*) is found in damp areas in Northern Australia, New Guinea, Indonesia, Malaysia, Philippines and China.

Further species currently included in Carolin's subsect. *Ebracteolatae*, such as *G. concinna* (Fig. 2C), *G. symonii* (Carolin) Carolin, *G. fascicularis*, the recently recognised *G. effusa* A.E.Holland (Holland 2015), and reinstated *G. pritzelii* (Barrett and Barrett 2018), were not successfully sequenced. Material was also unavailable for the very poorly understood *G. salmoniana* (F.Muell.) Carolin and *G. pallida* Carolin, which are only known from type collections from the Gascoyne and Pilbara regions in Western Australia. All of these species are retained within this newly circumscribed section due to the presence of diagnostic characters and the confirmed phylogenetic position of morphologically allied species; however, the position of *G. salmoniana* is equivocal as this species was originally placed in *Velleia* by Mueller (as *V. salmoniana* F.Muell.), most likely because its sepals are fused to the lower half of the ovary and the indusium lips are glabrous, unlike other species in this group.

Expansion of subg. *Monochila* (Goodenia Clade C)

Clade C is the most morphologically diverse clade in *Goodenia s.l.* and, while relationships between some of the subclades are unclear, each is generally supported as monophyletic. As such, subg. *Monochila* is expanded herein to include all members of Clade C, with most subclades formally named at the sectional level.

Typical sect. *Monochila* is easily recognised as all members (except the newly included *G. sericostachya* C.A.Gardner) have white, fan-shaped flowers (Fig. 2D) and a narrow indusium that is supported by a style covered in stiff, short, spreading hairs (Carolin 1992e). *G. sericostachya*, a narrow range endemic from Western Australia, was previously included in subsect. *Scaevolina* due to its dense indumentum of silver white hairs and pink fan-like flowers with a yellow throat (Fig. 8G). However, on close inspection it is evident that this species has the distinctive short hairs on the style and the narrow indusium that are diagnostic for sect. *Monochila,* confirming its affinity to other species in this clade. Two subsections are further recognised in sect. *Monochila*. The typical subsection includes all species with short white hairs on the style and capsular fruits, while the remaining species with short purple hairs on the style and a nut-like fruit are now included in a new subsection named herein as subsect. *Infracta* K.A.Sheph.

The majority of Carolin's (1992e) species included in his subsect. *Goodenia* fall within Goodenia Clade A; however, a small clade of yellow-flowered species were found to be nested within Goodenia Clade C (Jabaily et al. 2012; Gardner et al. 2016a). Don's (1834) sect. *Tetrathylax* G.Don, which previously only comprised the Western Australian narrow range endemic *G. quadrilocularis* (Figs 2A, 8D), is here resurrected and expanded to include this group, represented by several diploid and polyploid taxa (Peacock 1963) from eastern Australia. Sect. *Tetrathylax* is superficially similar to species in Clade A, due to the presence of yellow, bilabiate flowers, but this section is characterised by distinctive inflorescences comprising long, leafless, interrupted spikes, racemes or panicles where the upper pedicels have short, linear bracteoles close to the flowers with the lower ones being more distant. Carolin (1980) also noted that this group is characterised by unique seeds, that have a "sinuous-areolate" seed coat with the shape of the radial wall thickening as "type 4". *Goodenia rostrivalvis* Domin was not sequenced, but is included in sect. *Tetrathylax* due to its morphological similarity to allied species such as *G. decurrens* R.Br.

In Carolin's (1992e) *Flora of Australia* treatment, sect. *Coeruleae* comprises subsections *Scaevolina* and *Coeruleae*, and is represented by blue-flowered species of *Goodenia* where the septum of the ovary is at least 2/3 as long as the locule. In our molecular analyses, these subsections are each supported as monophyletic, but they never group together (Jabaily et al. 2018). Accordingly, they are treated as separate sections in our new classification. Sect. *Coeruleae* is re-circumscribed here to only include the members of the former subsect. *Coeruleae*, representing the blue-flowered perennial herbs and low subshrubs from southwest Western Australia with seeds that have a dry, membranous wing greater than 0.1 mm wide. This section now also includes *G. katabudjar* Cranfield & L.W.Sage and *G. lancifolia* L.W.Sage & Cranfield (Cranfield and Sage 1997; Sage 2000). The latter species was not placed in the phylogeny, along with *G. leptoclada* Benth., due to poor sequence results but both species share the diagnostic characters of this section.

Sect. *Scaevolina* represents the predominantly northern Australian blue-flowered perennials that have seeds with a narrow, mucilaginous wing c. 1 mm wide and has been expanded to include *G. azurea* subsp. *hesperia* L.W.Sage & Albr., *G. hartiana* L.W.Sage and *G. splendida* A.E.Holland & T.P.Boyle since the publication of Carolin's *Flora* treatment (Holland and Boyle 2002; Sage and Albrecht 2006).

Two species previously included in subsect. *Scaevolina* have a more southern distribution than typical. The first is the unusual fan-flowered *G. sericostachya* that is now included in sect. *Monochila*. The second is the rare species *G. arthrotricha* (Smith and Jones 2018), whose broader phylogenetic relationships remain unclear. In all molecular analyses, this species forms a well-supported clade with the short-range endemic *G. xanthotricha* (Fig. 8A), but their relationship to other subclades remains equivocal.

While *G. xanthotricha* was previously included in sect. *Goodenia*, Carolin (1992e) acknowledged that it was "a species difficult to place" noting that even though it has blue flowers, the seed coat ornamentation is "aculeate" rather than "colliculate-punctate" as seen in other members of subsect. *Scaevolina*. Furthermore, though members of the current sect. *Scaevolina* generally have an indusium that is longer than wide, the indusium in *G. arthrotricha* is wider than long, similar to that observed in many of the species of sect. *Coeruleae*. *Goodenia arthrotricha* and *G. xanthotricha* form a very weakly supported association with the southern *Coeruleae* clade in the nrITS analysis, but neither species has a seed with a dry wing > 0.1 mm wide (see the seed rim in Fig. 2F) that characterise this group. Both *G. arthrotricha* and *G. xanthotricha* are naturally rare, but somewhat surprisingly, their distribution overlaps as both species are found in a nature reserve situated on the Dandaragan plateau in Western Australia, although never observed as co-occurring (Western Australian Herbarium 1998-). One could hypothesise that their relatively close situation and morphological features that show some congruence to both sect. *Coeruleae* and *Scaevolina*, could suggest that one or both may be of possible hybrid origin. As these species are difficult to place systematically and no obvious synapomorphy supports them as distinct from other blue-flowered species, they currently remain unplaced within subg. *Monochila*.

Verreauxia is a small genus of three species from southwest Western Australia characterised by simple, unbranched and branched multicellular hairs, glandular hairs with multicellular heads (Carolin 1971), and a unilocular ovary that becomes indehiscent and nut-like in fruit. The closely allied monotypic *Pentaptilon* (Carolin 1992h), which occurs around the northernmost border between the South-West and Eremaean Botanical Provinces in Western Australia, has similarly unusual branched hairs; however, it was recognised as distinct due to its uniquely winged ovary and fruit, and morphologically distinct seeds. These genera group together in a monophyletic subclade within Clade C and so are recognised here as sect. *Verreauxia* in subg. *Monochila*.

The final monophyletic group that consistently placed sister to the rest of the morphologically diverse Clade C (Jabaily et al. 2018) is the genus *Velleia* characterised by inflorescences that are axillary dichasia, which form most of the plant habit (although sometimes flowers may be solitary), and a predominantly superior ovary (Fig. 2G). Carolin (1980) also noted that while the seeds in some *Velleia* showed similarity to various species of *Goodenia*, a number displayed a 'characteristic wrinkling'. Carolin's (1992g) infrageneric classification of *Velleia* recognised three sections, based on the presence of three sepals (sect. *Velleia*) or five, which may be either connate into a tube (sect. *Euthales*) or free (sect. *Menoceras*); however, in our analyses sect. *Menoceras* was shown to be paraphyletic and there was only moderate support for some of these former sections in the chloroplast analyses. As such, we propose here to reduce *Velleia* to a section of subg. *Monochila* and to not formally recognise any further groups within it. *Velleia parvisepta* Carolin and *V. perfoliata* R.Br., a narrow range endemic from New South Wales, while not sequenced are retained within this section as both species have the typical Form H inflorescence and sepals fused to near the base of the ovary, which are characters typical for sect. *Velleia*. It should be noted that while *V. perfoliata* is placed after *V. macrocalyx* de

Vriese in the proposed updated linear sequence for the genus (Table 2), Carolin (1992g) noted that this poorly known species had connate bracteoles that form a disk-like funnel unlike other species in his sect. *Velleia*. Three species in the former sect. *Menoceras* (*V. discophora* F.Muell., *V. panduriformis* A.Cunn. ex Benth. and *V. connata* F.Muell.) have similarly modified bracteoles to *V. perfoliata* (Table 2) and future sequencing of this species may confirm it is more closely allied to this group of taxa.

Conclusion

While this could be considered the final chapter of our detailed study of *Goodenia s.l.*, resulting in a new understanding and an updated classification of this captivating group, it is not likely to be the final word. *Goodenia s.l.* represents an outstanding clade for further studies, particularly of inflorescence and floral form, seed traits, and the potential impacts of adaptations on rates of diversification. These well sampled and resolved phylogenies also allow for the inclusion of Goodeniaceae in meta-studies of diversification patterns across Australia and in other biodiversity hotspots like the Southwest Australian Floristic Region (SWAFR) (Jabaily et al. 2014). Furthermore, this framework will support more in-depth studies at the species level to hopefully expedite the recognition of many new but as yet unnamed taxa.

Taxonomic treatment

In this present treatment, revised descriptions of infrageneric groups are provided with a synopsis of the species currently recognised therein, including updated nomenclatural changes. An updated key to genera in the family, including *Brunonia* (previously placed in the monotypic Brunoniaceae), and incorporating *Selliera*, *Pentaptilon*, *Velleia* and *Verreauxia* into *Goodenia* is also provided. A key is also provided to infrageneric groups as recognised in this paper.

Key to Genera (modified from Carolin et al. 1992, previously recognised genera in parentheses)

1a Anthers connate **2**
1b Anthers free **6**
2a Ovules and seeds more than 2 per locule; fruit a dehiscent capsule or fragmenting into articles, rarely an indehiscent beaked fruit **3**
2b Ovules and seeds 1 or 2 per locule; fruit an indehiscent nut, not beaked **4**
3a Leaves all cauline; indusium 2-lipped with stigmatic tissue on the outer surface .... ***Lechenaultia***
3b Leaves cauline and basal; indusium cup-like with stigmatic tissue inside .... ***Anthotium***

4a Inflorescence a solitary capitulum on a naked scape; corolla lobes connate towards the base.. ***Brunonia***

4b Inflorescence a loose, terminal raceme; corolla lobes free at the base............**5**

5a Corolla auriculate; hairs branched, rarely absent .... ***Dampiera***

5b Corolla without auricles; hairs simple ....***Scaevola filifolia* (*Diaspasis*)**

6a Ovules (and usually seeds) more than 2 per locule 7

6b Ovules and seeds 1 or 2 per locule **8**

7a Corolla with long, stiff bristles inside; seeds glossy, strophiolate, without a wing .... ***Coopernookia***

7b Corolla without bristles inside (may have hairs or enations); seeds dull, estrophiolate, with or without a wing .... ***Goodenia* (*Velleia*; *Selliera*)**

8a Plants glabrous or with simple hairs; flowers fan-like (rarely pseudoradial); ovary glabrous or with simple hairs, without wings **9**

8b Plants with branched and simple hairs; flowers bilabiate; ovary with dense multicellular hairs in 3 lines, sometimes winged...***Goodenia* (*Verreauxia; Pentaptilon*)**

9a Style with short, stiff hairs at 90°.................... ***Goodenia* (subg. *Monochila*)**

9b Style without short, stiff hairs at 90° **10**

10a Indusium broad (length equal to or shorter than width); fruit without a distinctive beak ....***Scaevola***

10b Indusium narrow (length longer than width); fruit with a distinctive beak up to 6 mm long...***Goodenia* (*Scaevola collaris*)**

Key to infrageneric groups within Goodenia (modified from Carolin et al. 1992, previously recognised taxa in brackets)

1a Sepals variously adnate to the ovary (ovary appears inferior) **2**

1b Sepals adnate to the ovary basally (ovary appears superior)........................**15**

2a Bracteoles present **3**

2b Bracteoles usually absent (if rarely present then < 3 mm long and deltoid)... **13**

3a Flowers fan-like...**4**

3b Flowers bilabiate 7

4a Ovules and seeds > 2...................**subg. *Goodenia* sect. *Goodenia* (*Selliera*)**

4b Ovules and seeds 1 or 2 ....**5**

5a Corolla lobes fused for more than 2/3 of their length, cream with a purplish-brown blush towards the base; fruit with a beak 1–6 mm long...**subg. *Goodenia* sect. *Goodenia* (*Scaevola collaris*)**

5b Corolla lobes free for more than 2/3 their length, white, cream or yellow with purplish spots or pink with a yellow throat; fruit without a beak **6**

6a Style with short white hairs at 90°; fruit a cylindrical to ovoid capsule ....**subg. *Monochila* sect. *Monochila* subsect. *Monochila***

6b Style with short purple hairs at 90°; fruit a globular to subglobular nut...**subg. *Monochila* sect. *Monochila* subsect. *Infracta***

7a Ovary with dense multicellular hairs in 3 lines; fruit sometimes winged ....**subg. *Monochila* sect. *Verreauxia* (*Verreauxia*; *Pentaptilon*)**

7b Ovary glabrous or with simple hairs; fruit not winged **8**

8a Ovules numerous, scattered over the surface of the placenta; seeds < 1 mm diameter ....**subg. *Porphyranthus* sect. *Porphyranthus***

8b Ovules and seeds in two rows in each locule; seeds >1 mm diameter...........**9**

9a Corolla blue, often yellowish in throat; seeds colliculate or reticulate........**10**

9b Corolla usually yellow or cream, rarely blue; seeds tuberculate or smooth and glossy..**11**

10a Subshrubs or herbs, usually densely glandular-hairy; seeds with narrow mucilaginous wing c. 0.1 mm wide .... **subg. *Monochila* sect. *Scaevolina***

10b Herbs with basal stock, glabrous or with simple or glandular hairs; seeds with membranous wing > 0.1 mm wide............**subg. *Monochila* sect. *Coeruleae***

11a Plants with or without a basal rosette of leaves; inflorescence a thyrse, raceme or spike with leafy bracts and bracteoles or with flowers solitary in leaf axils; seed coat various, not sinuous-areolate................................ **subg. *Goodenia***

11b Plants usually with a basal rosette of leaves; inflorescence a long, leafless, interrupted spike, raceme or panicle; seed coat sinuous-areolate.. **subg. *Monochila* sect. *Tetrathylax***

12a Erect or stoloniferous herbs or subshrubs with cauline leaves, glabrous or viscid with glandular and simple hairs...**subg. *Goodenia* sect. *Goodenia* and *G. nigrescens*, *G. cirrifica****

12b Decumbent or prostrate herbs with tufted or rosulate leaves, with simple, multicellular and/or glandular hairs, these often forming a dense, soft indumentum....**subg. *Goodenia* sect. *Rosulatae* and *G. wilunensis*, *G hirsuta****

13a Flowers fan-like, without auricles..**subg. *Porphyranthus* sect. *Porphyranthus* (sect. *Amphichila*)**

13b Flowers bilabiate, auriclate **14**

14a Flowers minute c. 1 mm long with a solitary ovule; fruit indehiscent.............................. **subg. *Porphyranthus* sect. *Porphyranthus* (*G. neogoodenia*)**

14b Flowers > 1 mm long with ≤ 30 ovules; fruit usually a dehiscent capsule....**subg. *Porphyranthus* sect. *Ebracteolatae* (subsect. *Ebracteolatae*; subsect. *Borealis*)**

15a Bracteoles present; inflorescences in dichasia or flowers solitary in axils of basal leaves......................................**subg. *Monochila* sect. *Velleia* (*Velleia*)**

15b Bracteoles absent; inflorescence a raceme or subumbel...**subg. *Porphyranthus* sect. *Ebracteolatae* (*G. macroplectra*)**

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* These species are included in subg. *Porphyranthus* sect. *Ebracteolatae*

Scaevola **L., Mant. Pl. 2: 145. 1771, *nom. cons.***

= *Diaspasis* R.Br., Prodr. 586. 1810, syn. nov. – Type: *D. filifolia* R.Br. ≡ *Scaevola filifolia* (R.Br.) K.A.Sheph.
= *Roemeria* Dennst., Schlüssel Hortus malab. 24. 1818, *nom. illeg.* [*non Roemeria* Medik., Ann. Bot. (Usteri) 1(3): 15. 1792] – Type: *R. lobelia* Dennst. ≡ *Scaevola taccada* (Gaertn.) Roxb.
= *Scaevola* sect. *Crossotoma* G.Don, Gen. hist. 3: 730. 1834 ≡ *Crossotoma* (G.Don) Spach., Hist. nat. vég. 9: 583. 1838 – Type: *Scaevola spinescens* R.Br.
= *Scaevola* sect. *Pogonanthera* G.Don, Gen. hist. 3: 729. 1834 ≡ *Pogonanthera* (G.Don) Spach, Hist. nat. vég. 9: 583. 1838, *nom. illeg.* (*non Pogonanthera* Blume, Flora 14: 520. 1831) – Type: *Scaevola striata* R.Br.
= *Scaevola* sect. *Xerocarpa* G.Don, Gen. hist. 3: 729. 1834 ≡ *Xerocarpa* (G.Don) Spach, Hist. nat. vég. 9: 583. 1838 – Type: *Scaevola crassifolia* Labill.
= *Pogonetes* Lindl., Intr. nat. syst. bot., ed. 2, 443. 1836, *nom. inval., nom. nud.*
= *Camphusia* de Vriese, Ned. Kruidk. Arch. 2: 148. 1851 – Type: *C. glabra* (Hook. & Arn.) de Vriese ≡ *Scaevola glabra* Hook. & Arn.
= *Merkusia* de Vriese, Ned. Kruidk. Arch. 2: 150. 1851 – Type: *M. crassifolia* (Labill.) de Vriese ≡ *Scaevola crassifolia* Labill.
= *Temminckia* de Vriese, Ned. Kruidk. Arch. 2: 141. 1851 – Type: *T. mollis* de Vriese ≡ *Scaevola mollis* Hook. & Arn.
= *Molkenboeria* de Vriese, Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2, 10: 38. 1854 – Type: *M. pilosa* (Benth.) de Vriese ≡ *Scaevola pilosa* Benth.
= *Nigromnia* Carolin, Nuytsia 1: 292 (1974) – Type: *N. globosa* Carolin ≡ *Scaevola globosa* (Carolin) Carolin.

Type (designated by W.R. Greuter et al. (eds), Reg. Veg. 118: 276. 1988). *Scaevola lobelia* L., *nom. illeg., typ. cons.* ≡ *Scaevola plumieri* (L.) Vahl.

Goodenia **Sm., Spec. bot. New Holland 15. 1793, *nom. cons.* (*fide* Shepherd et al. 2017; Applequist 2019)**[*]

Type. *G. ovata* Sm., *typ. cons.* (*fide* Shepherd et al. 2017; Applequist 2019).

Description. Perennial ***shrubs*** or ***subshrubs***, or annual or perennial ***herbs***, sometimes stoloniferous and rooting at nodes; glabrous, or with simple (sometimes multicellular) hairs, or viscid with glandular hairs. ***Leaves*** basal and/or cauline, petiolate or sessile, entire to pinnatifid, usually with axillary hairs. ***Inflorescence*** a raceme, thyrse, spike, panicle, subumbel, axillary dichasia, or flowers solitary in axils of basal leaves; pedicels sometimes articulate, rarely geniculate, with or without

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[*] For synonymy, see below under infrageneric taxa.

bracteoles. ***Sepals*** 5 or 3, fused or free, variously adnate to ovary. ***Corolla*** bilabiate or fan-like (lobes almost equal), white, cream, yellow, orange, pink, mauve, blue or purple; corolla-lobes usually winged, sometimes unequally; with hairs in the throat (rarely glabrous), sometimes with enations; often auriculate; sometimes with pouch or spur; stamens free, epigynous or hypogynous; style simple or 2–4-fid, glabrous or with simple hairs; indusia 1–4, 2-lipped, usually with bristles on lips; ovary inferior or superior, rarely winged, usually incompletely 2-locular with few to many ovules either in two rows or scattered over surface of the placentas, or solitary. ***Fruit*** a 2- or 4-valved capsule (rarely fleshy), 1-seeded nut, 4-seeded hard drupe or rarely a soft, indehiscent fruit with wings (*G. careyi*). ***Seeds*** flat or biconvex, usually with a rim or wing that is sometimes reduced.

Number of taxa and distribution. The genus has c. 251 taxa and is predominantly Australian. *Goodenia pilosa* extends to New Guinea, Indonesia, Malaysia, southern China and Philippines, while *G. armstrongiana*, *G. purpurascens* and *G. pumilio* extend to New Guinea and *G. koningsbergeri* occurs in India, Thailand, Cambodia, Malaysia and Indonesia according to Karthigeyan et al. (2009). Species previously included in *Selliera* also occur in coastal habitats in New Zealand and South America.

Goodenia Sm. subg. *Goodenia*

Description. ***Shrubs, subshrubs*** or ***herbs***, erect, decumbent or prostrate, sometimes stoloniferous and rooting at nodes. ***Leaves*** basal, cauline or both with the upper leaves sometimes smaller and narrower. ***Flowers*** in thyrses, racemes, spikes, or flowers solitary in leaf axils; bracts usually leafy; bracteoles usually present, pedicel infrequently geniculate, articulate or not. ***Corolla*** bilabiate or fan-like, usually yellow, sometimes white, cream or blueish purple, rarely pink; throat usually with scattered hairs, often with enations, not auriculate and often with a pouch. ***Style*** simple. ***Ovary*** with a variable septum from very short to 2/3 as long as locule; ovules in 2 rows in each locule or scattered, rarely solitary. ***Fruit*** a capsule with 2 valves, persistent or deciduous, rarely a fleshy fruit or 1-seeded nut. ***Seeds*** with a wing 0.1–0.2 mm wide and mucilaginous or obsolete.

Number of taxa and distribution. This subgenus currently includes 51 species, with 47 confined to Australia and three also occurring in New Zealand, Chile and southern Asia.

Goodenia Sm. subg. *Goodenia* sect. *Goodenia*

= *Selliera* Cav., Anales Hist. Nat. 1(1): 41, t. 5, fig. 2. 1799 ≡ *Goodenia* sect. *Selliera* (Cav.) G.Don, Gen. hist. 3: 725. 1834 – Type: *S. radicans* Cav. ≡ *Goodenia radicans* (Cav.) Pers.

≡ *Goodenia* sect. *Ochrosanthus* G.Don, Gen. hist. 3: 724. 1834 – Type (designated by Carolin in George (ed.), Fl. Australia 35: 330. 1992): *G. ovata* Sm.

= *Picrophyta* F.Muell., Linnaea 25: 421. 1853 – Type: *P. albiflora* (Schltdl.) F.Muell. ≡ *Goodenia albiflora* Schltdl.

= *Goodenia* sect. *Eugoodenia* Benth., *Fl. Austral.* 4: 51, 57. 1868, *nom. inval.*

≡ *Goodenia* sect. *Goodenia* ser. *Bracteolatae* Benth., Fl. Austral. 4: 52, 59. 1868 ≡ *Goodenia* sect. *Goodenia* subsect. *Bracteolatae* (Benth.) K.Krause in H.G.A. Engler (ed.), Pflanzenr. 54(277): 46. 1912 – Type (designated by Carolin in George (ed.), Fl. Australia 35: 331. 1992): *G. ovata* Sm.

= *Goodenoughia* F.Muell., Syst. Census Austral. pl. 88. 1882, *nom. inval., pro syn.*

≡ *Goodenoughia* Siebert & Voss, Vilm. Blumengärtn. ed 3. 1(1): 559. 1894, *nom. illeg., nom. superfl.* – Type: *Goodenoughia ovata* (Sm.) Siebert & Voss ≡ *Goodenia ovata* Sm.

= *Goodenia* ser. *Suffruticosae* K.Krause in H.G.A.Engler (ed.), Pflanzenr. 54: 46, 59. 1912 – Type: *G. ovata* Sm.

Description. ***Shrubs, subshrubs*** or ***herbs,*** glabrous or viscid with glandular and simple hairs. ***Leaves*** usually cauline. ***Flowers*** in leafy thyrses, racemes, spikes, or solitary in leaf axils; pedicel sometimes articulate. ***Corolla*** bilabiate or fan-like.

Number of taxa and distribution. This section contains 23 species, most of which are Australian, while *G. heenanii* and *G. radicans* are present in New Zealand with the latter species also found in South America. The only other extra Australian species is *G. koningsbergeri*, which occurs in India, Thailand, Cambodia, Malaysia and Indonesia.

Included species. *G. albiflora* Schltdl., *G. amplexans* F.Muell., *G. benthamiana* Carolin, *G. brunnea* Carolin, *G. calcarata* (F.Muell.) F.Muell., *G. chambersii* F.Muell., *G. collaris* (F.Muell.) K.A.Sheph., *G. exigua* F.Muell., *G. grandiflora* Sims, *G. heenanii* K.A.Sheph., *G. kingiana* Carolin, *G. koningsbergeri* (Back.) Back. ex Bold., *G. laevis* Benth., *G. laevis* subsp. *humifusa* L.W.Sage, *G. laevis* Benth. subsp. *laevis*, *G. macmillanii* F.Muell., *G. ovata* Sm., *G. phillipsiae* Carolin, *G. radicans* (Cav.) Pers., *G. saccata* Carolin, *G. stirlingii* F.M.Bailey, *G. valdentata* P.J.Lang, *G. varia* R.Br., *G. vernicosa* J.M.Black, *G. viscida* R.Br.

Goodenia **subg.** ***Goodenia*** **sect.** ***Rosulatae*** **(K.Krause) K.A.Sheph., comb. et stat. nov.**

urn:lsid:ipni.org:names:77209991-1

= *Goodenia* ser. *Rosulatae* K.Krause in H.G.A.Engler (ed.), Pflanzenr. 54: 46, 52. 1912 – Type (designated by Carolin in George (ed.), Fl. Australia 35: 331. 1992): *G. geniculata* R.Br.

= *Catospermum* Benth., Hooker's Icon. Pl. 11: t. 1028. 1867 – Type: *C. muelleri* Benth., *nom. illeg.* ≡ *Goodenia goodeniacea* (F.Muell.) Carolin.

Description. ***Herbs*** or occasionally ***subshrubs,*** usually with multicellular hairs sometimes becoming glabrescent, or rarely with simple and glandular hairs. ***Leaves*** basal and/or cauline. ***Flowers*** usually in racemes or solitary in leaf axils; pedicels usually not articulate. ***Corolla*** bilabiate.

Number of taxa and distribution. This section includes 28 species found in every state of Australia across a range of biomes with some species extending into arid central inland regions.

Included species. *G. affinis* de Vriese, *G. arenicola* Carolin, *G. atriplexifolia* A.E.Holland & T.P. Boyle, *G. blackiana* Carolin, *G. centralis* Carolin, *G. convexa* Carolin, *G. delicata* Carolin, *G. disperma* Mueller, *G. dyeri* K.Krause, *G. expansa* A.E.Holland & T.P.Boyle, *G. fordiana* Carolin, *G. geniculata* R.Br., *G. glabra* R.Br., *G. goodeniacea* (F.Muell.) Carolin, *G. hederacea* Sm., *G. hederacea* subsp. *alpestris* (K.Krause) Carolin, *G. hederacea* Sm. subsp. *hederacea*, *G. heterophylla* Sm., *G. heterophylla* subsp. *eglandulosa* Carolin, *G. heterophylla* Sm. subsp. *heterophylla*, *G. heterophylla* subsp. *montana* Carolin, *G. heterophylla* subsp. *teucriifolia* (F.Muell.) Carolin, *G. lanata* R.Br., *G. mueckeana* F.Muell., *G. peacockiana* Carolin, *G. robusta* (Benth.) K.Krause, *G. rotundifolia* R.Br., *G. rupestris* Carolin, *G. schwerinensis* Carolin, *G. stephensonii* F.Muell., *G. tripartita* Carolin, *G. viridula* Carolin, *G. willisiana* Carolin, *G. xanthosperma* F.Muell.

Goodenia subg. *Porphyranthus* (G.Don) K.A.Sheph., comb. et stat. nov.

urn:lsid:ipni.org:names:77209992-1

≡ *Goodenia* sect. *Porphyranthus* G.Don, Gen. hist. 3: 725. 1834 – Type (designated by Carolin in George (ed.), Fl. Australia 35: 330. 1992): *G. purpurascens* R.Br.

Description. ***Subshrubs*** or ***herbs,*** erect or decumbent, sometimes with a basal stock. ***Leaves*** basal, cauline or both, sometimes with smaller stem leaves. ***Flowers*** in thyrses, racemes, or subumbels, rarely head-like or solitary in axils; bracts leafy or bracteose; bracteoles present or absent; pedicels maybe articulate. ***Corolla*** bilabiate, rarely fan-like, yellow, mauve, brownish, purple, pink, or blue; throat glabrous or with long stiff hairs sometimes arranged in rows and confluent towards base, often without enations, often with auricules; pocket usually inconspicuous. ***Style*** simple or 3- or 4-fid. ***Ovary*** with septum short to 2/3 locule length; ovules in two rows in each locule or scattered over the surface of the placentas. ***Fruit*** a capsule, valves 2, persistent or deciduous, entire or bifid. ***Seeds*** with a prominent rim or a mucilaginous wing.

Number of taxa and distribution. This subgenus consists of 121 species that are predominantly Australian with a few species such as *G. pumilio* and *G. armstrongiana* extending to New Guinea, while *G. pilosa* is widespread through southern Asia and China.

Goodenia subg. *Porphyranthus* sect. *Porphyranthus* G.Don

= *Goodenia* sect. *Amphichila* DC., Prodr. 5: 516. 1836 – Type: *G. pumilio* R.Br.

= *Neogoodenia* C.A.Gardner & A.S.George, J. Roy. Soc. Western Australia 46: 138, fig. 6. 1963 – Type: *N. minutiflora* C.Gardner & A.S.George ≡ *Goodenia neogoodenia* Carolin.

Description. ***Herbs. Leaves*** basal, cauline or both. ***Flowers*** in thyrses, racemes, or loose panicles, rarely head-like or solitary in axils, bracts often leaf-like in lower parts becoming linear distally; pedicel usually with bracteoles. ***Corolla*** bilabiate or rarely fan-like, yellow, mauve to pinkish, or deep red, glabrous inside or with a few hairs. ***Style*** simple. ***Ovary*** with more than 30 ovules scattered over placentas. ***Seeds*** mostly less than 1 mm wide, glossy, with a prominent rim or wing *c.* 0.1 mm wide or obsolete.

Number of taxa and distribution. A section of 26 species, mostly in northern and central Australia with *G. purpurascens* and *G. pumilio* also present in New Guinea. Many species are confined to seasonally wet habitats.

Included species. *G. berringbinensis* Carolin, *G. bicolor* F.Muell. ex Benth., *G. chthonocephala* Carolin, *G. claytoniacea* F.Muell. ex Benth., *G. corralina* L.W.Sage & K.A.Sheph.; *G. cravenii* R.L.Barrett & M.D.Barrett, *G. cylindrocarpa* Albr., *G. gloeophylla* Carolin, *G. gracilis* R.Br., *G. gypsicola* Symon; *G. halophila* Albr., *G. humilis* R.Br., *G. kakadu* Carolin, *G. lamprosperma* F.Muell., *G. lyrata* Carolin, *G. macbarronii* Carolin, *G. minutiflora* F.Muell., *G. modesta* J.M.Black, *G. neogoodenia* Carolin, *G. nocoleche* Pellow & J.L.Porter, *G. oenpelliensis* R.L.Barrett, *G. paniculata* Sm., *G. pumilio* R.Br., *G. purpurascens* R.Br., *G. rosulata* Domin, *G. viscidula* Carolin.

Goodenia subg. *Porphyranthus* sect. *Ebracteolatae* (K.Krause) K.A.Sheph., comb. et stat. nov.

urn:lsid:ipni.org:names:77209993-1

≡ *Goodenia* subsect. *Ebracteolatae* K.Krause in H.G.A.Engler (ed.), Pflanzenr. 54: 46. 1912 – Type (here designated): *Goodenia pinnatifida* Schltdl.

= *Calogyne* R.Br., Prodr. 579. 1810 ≡ *Goodenia* ser. *Calogyne* (R.Br.) Carolin, Fl. Australia 35: 331. 1992 – Type: *C. pilosa* R.Br. ≡ *Goodenia pilosa* (R.Br.) Carolin.

= *Distylis* Gaudich., Voy. Uranie 10: 460, t. 80. 1829 – Type: *D. berardiana* Gaudich. ≡ *Goodenia berardiana* (Gaudich.) Carolin.

= *Balingayum* Blanco, Fl. Filip. 187. 1837 – Type: *Balingayum decumbens* Blanco = *Goodenia pilosa* (R.Br.) Carolin.

= *Aillya* de Vriese, Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2, 10: 75. 1854 – Type: *A. umbellata* (Vriese) Vriese = *Goodenia pulchella* Benth.

= *Goodenia* sect. *Goodenia* ser. *Foliosae* Benth., Fl. Austral. 4: 53, 69. 1868 – Type (designated by Carolin in George (ed.), Fl. Australia 35: 331. 1992): *G. strangfordii* F.Muell.

= *Goodenia* ser. *Pedicellosae* Benth., Fl. Austral. 4: 54, 73. 1868 – Type (designated by Carolin in George (ed.), Fl. Australia 35: 331. 1992): *G. cycloptera* R.Br.

= *Symphyobasis* K.Krause, Pflanzenr. 54: 40, fig. 11. 1912 – Type: *S. macroplectra* (F.Muell.) K.Krause ≡ *Goodenia macroplectra* (F.Muell.) Carolin.

= *Goodenia* subsect. *Borealis* Carolin ser. *Borealis* in A.S.George (ed.), Fl. Australia 35: 331 (1992) – Type: *G. sepalosa* F.Muell. ex Benth.

Description. Low ***shrubs*** or ***herbs***. ***Leaves*** usually basal (sometimes ephemeral) and/or cauline. ***Flowers*** usually in racemes or subumbels with leafy bracts; pedicel usually without bracteoles. ***Corolla*** bilabiate, yellow, mauve or brownish purple, with hairs inside arranged in rows often becoming confluent towards base. ***Style*** simple or 3- or 4-fid. ***Ovary*** with 30 or less ovules, in two rows in each locule. ***Seeds*** usually more than 1.5 mm wide, rarely glossy, wing prominent and usually mucilaginous.

Number of taxa and distribution. This section includes 95 species across Australia with *G. armstrongiana* extending northwards into New Guinea. The annual *G. pilosa* subsp. *pilosa* extends from Australia to Indonesia, Papua New Guinea, Malaysia, and the Philippines while the perennial *G. pilosa* subsp. *chinensis* is found in China and Vietnam.

Included species. *G. anfracta* J.M.Black, *G. angustifolia* Carolin, *G. arachnoidea* Carolin, *G. argillacea* Carolin, *G. armitiana* F.Muell, *G. armstrongiana* de Vriese, *G. asteriscus* P.J.Lang, *G. berardiana* (Gaudich.) Carolin, *G. brachypoda* (F.Muell. ex Benth.) Carolin, *G. byrnesii* Carolin, *G. campestris* Carolin, *G. cirrifica* F.Muell., *G. concinna* Benth., *G. coronopifolia* R.Br., *G. corynocarpa* F.Muell.; *G. crenata* Carolin & L.W.Sage; *G. cusackiana* F.Muell., *G. cycloptera* R.Br., *G. debilis* A.E.Holland & T.P.Boyle; *G. durackiana* Carolin; *G. effusa* A.E.Holland, *G. elaiosoma* Cowie; *G. elongata* Labill., *G. fascicularis* F.Muell. & Tate; *G. faucium* Carolin; *G. filiformis* R.Br., *G. forrestii* F.Muell., *G. gibbosa* Carolin, *G. glandulosa* K.Krause, *G. glauca* F.Muell., *G. granitica* L.W.Sage & K.A.Sheph., *G. havilandii* Maiden & Betche, *G. heatheriana* L.W.Sage, *G. heppleana* (W.Fitzg.) Carolin, *G. heterochila* F.Muell., *G. heteromera* F.Muell., *G. heterotricha* M.D.Barrett & R.L.Barrett, *G. hirsuta* F.Muell., *G. hispida* R.Br., *G. holtzeana* (Specht) Carolin, *G. integerrima* Carolin, *G. inundata* L.W.Sage & J.P.Pigott, *G. iyouta* Carolin, *G. janamba* Carolin, *G. jaurdiensis* L.W.Sage & K.A.Sheph., *G. krauseana* Carolin, *G. larapinta* Tate, *G. leiosperma* Carolin, *G. lobata* Ising, *G. lunata* J.M.Black, *G. macroplectra* (F.Muell.) Carolin, *G. maideniana* W.Fitzg., *G. malvina* Carolin, *G. maretensis* R.L.Barrett, *G. megasepala* Carolin, *G. micrantha* Hemsl. ex Carolin, *G. microptera* F.Muell., *G. mimuloides* S.Moore, *G. muelleriana* Carolin, *G. neglecta* (Carolin) Carolin, *G. nigrescens* Carolin, *G. nuda* E.Prtiz., *G. occidentalis* Carolin, *G. ochracea* Carolin, *G. odonnellii* F.Muell., *G. pallida* Carolin, *G. pascua* Carolin, *G. pedicellata* L.W.Sage & K.W.Dixon, *G. pilosa* (R.Br.) Carolin, *G. pilosa* (R.Br.) Carolin subsp. *pilosa*, *G. pilosa* subsp. *chinensis* (Benth.) D.G.Howarth & D.Y.Hong, *G. pinnatifida* Schltdl., *G. porphyrea* (Carolin) Carolin, *G. potamica* Carolin, *G. pritzelii* Domin, *G. prostrata* Carolin, *G. psammophila* L.W.Sage & M.D.Barrett, *G. psammophila* subsp. *hiddinsiana* L.W.Sage & M.D.Barrett, *G. psammophila* L.W.Sage & M.D.Barrett subsp. *psammophila*, *G. pulchella* Benth., *G. purpurea* (F.Muell.) Carolin, *G. pusilla* (de Vriese) de Vriese, *G. pusilliflora* F.Muell., *G. quadrifida* (Carolin) Carolin, *G. quasilibera* Carolin, *G. redacta* Carolin, *G. salina* L.W.Sage & K.A.Sheph., *G. salmoniana* (F.Muell.) Carolin, *G. sepalosa* F.Muell. ex Benth., *G. sepalosa* var. *glandulosa* Carolin, *G. sepalosa* F.Muell. ex Benth. var. *sepalosa*, *G. stellata* Carolin, *G. strangfordii* F.Muell., *G. subauriculata* C.T.White, *G. symonii* (Carolin) Carolin, *G. tenuiloba* F.Muell., *G. triodiophila* Carolin, *G. turleyae* L.W.Sage & K.A.Sheph., *G. vilmoriniae* F.Muell., *G. virgata* Carolin, *G. wilunensis* Carolin.

Goodenia **subg.** ***Monochila*** **(G.Don) Carolin, Fl. Australia 35: 330. 1992.**

= *Goodenia* sect. *Monochila* G.Don, Gen. hist. 3: 725. 1834.

Type. (designated by Carolin in George (ed.), Fl. Australia 35: 330. 1992): *G. scapigera* R.Br.

Description. ***Shrubs, subshrubs*** or ***herbs,*** erect or decumbent, sometimes with a basal stock. ***Leaves*** basal, cauline or both. ***Flowers*** in axillary dichasia or terminal thyrses, racemes or spikes; bracts leafy or bracteose; bracteoles present; pedicels may be articulate. ***Corolla*** bilabiate or fan-like, white (sometimes with purple spots at the base of the lobes), yellow, blue or blueish-purple or rarely pink to mauve; throat glaborous, sometimes with stiff hairs, with or without enations, with or without auricles; pouch inconspicuous or prominent to 1/2 ovary length. ***Style*** simple. ***Ovary*** with septum *c*. 2/3 locule length or 1 locular; ovules usually in 2-rows, rarely solitary. ***Fruit*** a capsule with 2 valves, persistent or deciduous, rarely indehiscent and nutlike. ***Seeds*** with or without a membranous or mucilaginous wing.

Number of taxa and distribution. The subgenus *Monochila* includes 58 species across six sections. Western Australia is a centre of diversity for this group with species from sect. *Velleia* also found in Eastern Australia and one species present in New Guinea.

Goodenia **subg.** ***Monochila*** **sect.** ***Monochila*** **G.Don, Gen. hist. 3: 725. 1834.**

Description. ***Shrubs, subshrubs*** or ***herbs***. ***Leaves*** basal, cauline or both. ***Flowers*** in thyrses or spikes; usually with bracteose bracts; bracteoles present. ***Sepals*** equal. ***Corolla*** fan-like, white with brown or purple spots at the base of each lobe or pink with a bright yellow throat, with stiff hairs in throat, enations absent, without auricles; pouch inconspicuous, to 1/2 ovary length. ***Ovary*** 2-locular with ovules solitary or to 40, usually in 2-rows in each locule. ***Fruit*** either a capsule with valves bifid or indehiscent and nutlike. ***Seeds*** to c.1 mm, wing < 0.5 mm and mucilaginous or obsolete.

Number of taxa and distribution. A Western Australian section of 10 species.

Goodenia **subg.** ***Monochila*** **sect.** ***Monochila*** **subsect**. ***Monochila***

= *Stekhovia* de Vriese, Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2, 10: 166. 1854. – Type: *S. scapigera* (R.Br.) de Vriese ≡ *Goodenia scapigera* R.Br.

Description. ***Style*** with simple white hairs. ***Ovary*** with 12–40 ovules. ***Fruit*** a cylindrical to ovoid capsule.

Number of taxa and distribution. A subsection of six species endemic to south-west Western Australia.

Included species. *G. decursiva* W.Fitzg., *G. elderi* F.Muell. & Tate, *G. pinifolia* de Vriese, *G. scapigera* R.Br., *G. scapigera* subsp. *graniticola* L.W.Sage, *G. scapigera* R.Br.

subsp. *scapigera*, *G. sericostachya* C.A.Gardner, *G. watsonii* F.Muell. & Tate, *G. watsonii* subsp. *glandulosa* Carolin, *G. watsonii* F.Muell. & Tate subsp. *watsonia*.

Goodenia **subg.** ***Monochila*** **sect.** ***Monochila*** **subsect.** ***Infracta*** **K.A.Sheph., subsect. nov.**

= *Scaevola* ser. *Parviflorae* Benth., Fl. Austral. 4: 86, 103. 1868 – Type: *S. fasciculata* Benth. ≡ *Goodenia fasciculata* (Benth.) Carolin.

Type. *G. helmsii* (E.Pritz.) Carolin.

Description. ***Style*** with stiff purple hairs. ***Ovary*** with 1–3 ovules. ***Fruit*** a globular to subglobular nut.

Etymology. The name is from the Latin *infractus* (unbroken) in reference to members of this section having a hard, nut-like fruit.

Number of taxa and distribution. A subsection of four species endemic to southwest Western Australia.

Included species. *G. drummondii* Carolin, *G. drummondii* Carolin subsp. *drummondii*, *G. drummondii* subsp. *megaphylla* L.W.Sage, *G. fasciculata* (Benth.) Carolin, *G. helmsii* (E.Pritz.) Carolin, *G. stenophylla* F.Muell.

Goodenia **subg.** ***Monochila*** **sect.** ***Scaevolina*** **(Carolin) K.A.Sheph., comb. et stat. nov.**

urn:lsid:ipni.org:names:77209994-1

≡ *Goodenia* subsect. *Scaevolina* Carolin in A.S.George (ed.), Fl. Austral. 35: 331. 1992 – Type: *G. scaevolina* F.Muell.

Description. ***Subshrubs*** or ***herbs***. ***Leaves*** basal or cauline, basal leaves sometimes absent in mature plants. ***Flowers*** in thyrses or racemes comprising at least 1/2 to 2/3 of the plant, with leafy bracts; bracteoles present. ***Sepals*** equal. ***Corolla*** bilabiate or becoming fan-like, blue usually with a yellow or whitish throat, usually with hairs on margins and in the throat, enations prominent; scarcely auriculate; pouch usually prominent. ***Ovary*** 2-locular with 20–60 ovules in two rows in each locule. ***Fruit*** a capsule, valves entire or bifid. ***Seeds*** > 1.5 mm wide, wing *c.* 0.1 mm wide and mucilaginous or obsolete.

Number of taxa and distribution. A section of eight species from northern and central Australia extending southwards into the Eremaean bioregion of Western Australia.

Included species. *G. azurea* F.Muell., *Goodenia azurea* F.Muell. subsp. *azurea*, *G. azurea* subsp. *hesperia* L.W.Sage & Albr., *G. eremophila* E.Pritz., *G. hartiana* L.W.Sage, *G. ramelii* F.Muell., *G. scaevolina* F.Muell., *G. splendida* A.E.Holland & T.P.Boyle, *G. stobbsiana* F.Muell., *G. suffrutescens* Carolin.

Goodenia **subg.** ***Monochila*** **sect.** ***Coeruleae*** **(Benth.) Carolin in A.S.George (ed.), Fl. Australia 35: 330. 1992 (as** ***'Caeruleae'*****)**

≡ *Goodenia* subg. *Goodenia* ser. *Coeruleae* Benth., Fl. Austral. 4: 53, 65. 1868 (as '*Caeruleae*') ≡ *Goodenia* subg. *Goodenia* subsect. *Coeruleae* (Benth.) Carolin, Fl. Australia 35: 330. 1992 (as '*Caeruleae*') – Type (designated by Carolin in George (ed.), Fl. Australia 35: 330. 1992): *G. coerulea* R.Br.

Description. ***Herbs*** with basal stock. ***Leaves*** basal or cauline. ***Flowers*** in racemes arising from axils of basal leaves with bracteose or leafy bracts; bracteoles present. ***Sepals*** equal. ***Corolla*** bilabiate; blue usually with a yellow or whitish throat, usually with hairs in the throat, enations present or absent; scarcely auriculate; pouch present or absent. ***Ovary*** 2-locular with 20–40 ovules in two rows in each locule. ***Fruit*** a capsule, valves entire or bifid. ***Seeds*** > 1.5 mm wide, wing > 0.1 mm wide dry, hyaline or obsolete.

Number of taxa and distribution. A section of 11 species from south-west Western Australia.

Included species. *G. coerulea* R.Br., *G. eatoniana* F.Muell., *G. glareicola* Carolin, *G. hassallii* F.Muell., *G. incana* R.Br., *G. katabudjar* Cranfield & L.W.Sage, *G. lancifolia* L.W.Sage & Cranfield, *G. leptoclada* Benth., *G. perryi* C.A.Gardner ex Carolin, *G. pterigosperma* R.Br., *G. trichophylla* de Vriese ex Benth.

Goodenia **subg.** ***Monochila*** **sect.** ***Tetrathylax*** **G.Don, Gen. hist. 3: 725. 1834**

≡ *Tetrathylax* (G.Don) de Vriese, Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2, 10: 164. 1854 (as '*Tetraphylax*') – Type: *T. quadrilocularis* (R.Br.) Vriese ≡ *Goodenia quadrilocularis* R.Br.

= *Goodenia* sect. *Goodenia* ser. *Racemosae* Benth., Fl. Austral. 4: 51, 57 (1868) – Type (designated by Carolin in George (ed.), Fl. Australia 35: 331. 1992): *G. decurrens* R.Br.

Description. ***Subshrubs*** or ***herbs***. ***Leaves*** basal or if cauline usually narrower and smaller. ***Flowers*** in thyrse-like panicles, racemes or spikes with bracteose bracts; bracteoles present. ***Sepals*** equal. ***Corolla*** bilabiate, yellow, lemon or rarely orange, hairs in throat, enations present; scarcely auriculate to auriculate. ***Ovary*** 2-locular with 15–65 ovules in two rows in each locule. ***Fruit*** a capsule, valves usually ± bifid or rarely entire. ***Seeds*** 1–1.8 mm long, wing c. 0.1 mm wide and mucilaginous or with a rim.

Number of taxa and distribution. A section of nine species present in coastal and highland areas including the Blue Mountains in eastern Australia and *G. quadrilocularis* from near Cape le Grand in south-west Western Australia.

Included species. *G. bellidifolia* Sm., *G. bellidifolia* subsp. *argentea* Carolin, *G. bellidifolia* Sm. subsp. *bellidifolia*, *G. decurrens* R.Br., *G. dimorpha* Maiden & Betche, *G. dimorpha* var. *angustifolia* Maiden & Betche, *G. dimorpha* Maiden & Betche var. *dimorpha*, *G. glomerata* Maiden & Betche, *G. lineata* J.H.Willis, *G. quadrilocularis* R.Br., *G. racemosa* F.Muell., *G. racemosa* var. *latifolia* Carolin, *G. racemosa* F.Muell. var. *racemosa*, *G. rostrivalvis* Domin, *G. stelligera* R.Br.

Note. Don (1834) recognised the section *Tetrathylax* (meaning four – pouch) to include *G. quadrilocularis*. The name was formed providing the Greek and Latin translations for *tetras* (four-fold) and *thylax* (a cell) in recognition of the 4-celled condition of the capsule. de Vriese treated the section at generic rank with the incorrect spelling '*Tetraphylax*', which was followed by subsequent authors until corrected by Carolin (1992e).

***Goodenia* subg. *Monochila* sect. *Verreauxia* (Benth.) K.A.Sheph., comb. et. stat. nov.**

urn:lsid:ipni.org:names:77210076-1

≡ *Verreauxia* Benth., Fl. Austral. 4: 105. 1868, syn. nov. – Type: *V. verreauxii* (de Vriese) Carolin = *Dampiera verrauxii* de Vriese.

= *Pentaptilon* E.Pritz., Bot. Jahrb. Syst. 35(4): 564, fig. 65. 1905, syn. nov. – Type: *P. careyi* (F.Muell.) Pritzel ≡ *Catospermum careyi* F.Muell. ≡ *Goodenia careyi* (F.Muell.) K.A.Sheph.

Description. ***Herbs or shrubs***. ***Leaves*** basal and/or cauline, with unique branched hairs. ***Flowers*** in loose or spike-like, often a branched thyrse on a terminal scape with bracteose bracts; bracteoles present. ***Sepals*** equal. ***Corolla*** bilabiate, yellow, with or without hairs inside throat, enations absent; scarcely auriculate; pouch inconspicuous to short. ***Ovary*** 1- to 2-locular, with unique reddish or golden multicellular hairs between 3 of the sepaline ribs that may be winged (in *G. careyi*), with 1–6 ovules per locule scattered over placentas. ***Fruit*** a compressed, hairy nut or an indehiscent capsule with wings. ***Seeds*** 1.7–2.5 mm long, wing obsolete.

Number of taxa and distribution. A section of four species endemic to south-western Australia.

Included species. *G. careyi* (F.Muell.) K.A.Sheph., *G. etheira* K.A.Sheph., *G. reinwardtii* (de Vriese) K.A.Sheph., *G. verreauxii* (de Vriese) K.A.Sheph.

***Goodenia* subg. *Monochila* sect. *Velleia* (Sm.) K.A.Sheph., comb. et. stat. nov.**

urn:lsid:ipni.org:names:77210077-1

≡ *Velleia* Sm., Trans. Linn. Soc. London, Bot. 4: 217. 1798, syn. nov. – Type: *V. lyrata* R.Br.

= *Euthales* R.Br., Prodr. 579. 1810 ≡ *Velleia* sect. *Euthales* (R.Br.) Carolin, Proc. Linn. Soc. New South Wales 92(1): 28. 1967 – Type: *E. trinervis* (Labill.) R.Br. ≡ *Goodenia trinervis* (Labill.) K.A. Sheph.

= *Menoceras* (R.Br.) Lindl., Veg. kingd. 685. 1846 ≡ *Velleia* sect. *Menoceras* R.Br., Prodr. 580. 1810 – Type: (designated by Carolin, Proc. Linn. Soc. New South Wales 92(1): 34. 1967): *Velleia paradoxa* R.Br. ≡ *Goodenia paradoxa* (R.Br.) K.A.Sheph.

= *Velleia* sect. *Aceratia* F.Muell., Trans. Philos. Soc. Victoria 1: 17. 1854 – Type: *V. connata* F.Muell. ≡ *Goodenia connata* (F.Muell.) K.A.Sheph.
= *Antherostylis* C.A.Gardner, J. Roy. Soc. Western Australia 19: 91. 1934 – Type: *A. calcarata* C.Gardner ≡ *G. arguta* (R.Br.) K.A. Sheph.

Description. ***Herbs*** with short stems. ***Leaves*** basal or cauline. ***Flowers*** in axillary dichasia with scapes erect to prostrate or flowers solitary in axils usually with bracteose bracts; bracteoles present and sometimes disc-like. ***Sepals*** equal or adaxial one larger. ***Corolla*** bilabiate yellow, orange, mauve, pink or white, with or without hairs in the throat, enations absent or present, auriculate, pouch absent or present, sometimes forming a spur. ***Ovary*** 2-locular with 4–25 ovules. ***Fruit*** a capsule with with 2 or 4 valves. ***Seeds*** 1.5–6 mm long, wing 0.5–2 mm wide or with a thickened rim.

Number of taxa and distribution. The section includes 20 species, of which 19 are endemic to Australia with *G. mystrophylla* K.A.Sheph. (previously *Velleia spathulata*) also present in New Guinea.

Included species. *G. arguta* (R.Br.) K.A.Sheph., *G. brendannarum* K.A.Sheph., *G. capillosa* K.A.Sheph., *G. caroliniana* K.A.Sheph., *G. connata* (F.Muell.) K.A.Sheph., *G. cycnopotamica* (F.Muell.) K.A.Sheph., *G. daviesii* (F.Muell.) K.A.Sheph., *G. discophora* (F.Muell.) K.A.Sheph., *G. subsolana* K.A.Sheph., *G. glabrata* (Carolin) K.A.Sheph., *G. macrocalyx* (de Vriese) K.A.Sheph., *G. macrophylla* (Lindl.) F.Muell., *G. montana* (Hook.f.) K.A.Sheph., *G. mystrophylla* K.A.Sheph., *G. panduriformis* (A.Cunn. ex Benth.) K.A.Sheph., *G. paradoxa* (R.Br.) K.A.Sheph., *G. parvisepta* (Carolin) K.A.Sheph., *G. perfoliata* (R.Br.) K.A.Sheph., *G. rosea* (S.Moore) K.A.Sheph., *G. trinervis* (Labill.) K.A.Sheph.

Incertae sedis

Goodenia arthrotricha Benth., Fl. Austral. 4: 62. 1868 – Lectotype (designated by Carolin, Telopea 3(4): 539. 1990): Australia. Western Australia. S.W. Australia, 1848, *J.Drummond 190* (K 000215740 [image!]; isolectotype: BM 001041473 [image!]; probable isolectotype: MEL 23036 [image!], MEL 23037 [image!]).
Goodenia xanthotricha de Vriese, Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2, 10: 155. 1854 – Type citation: "Nov. Holl. Verreaux. (*Herb. propr.*)". Type: *n.v.*

New Combinations and reinstated taxa

Goodenia arguta (R.Br.) K.A. Sheph., comb. nov.

urn:lsid:ipni.org:names:77210078-1

≡ *Velleia arguta* R.Br., Prodr. 580. 1810 – Holotype: Australia: Western Australia. Base of the Mountains near Inlet No. XII South Coast, *s. dat.*, *R.Brown s.n.* [Bennett no. 2548] (BM 000949843 [image!]).

Goodenia brendannarum **K.A.Sheph., nom. nov.**

urn:lsid:ipni.org:names:77210079-1

≡ *Velleia macrophylla* var. *foliosa* Benth. Fl. Austral. 4: 48. 1868 ≡ *Velleia foliosa* (Benth.) K.Krause in H.G.A.Engler (ed.), Pflanzenr. 54: 40. 1912 – Lectotype (designated by Carolin, Proc. Linn. Soc. New South Wales 92(1): 33 (1967): Australia. Western Australia. S.W. Australia, *J.Drummond 182* (K 000215384 [image!]; isolectotypes: MEL 9736 [image!], NSW *n.v.*, P 00698807 [image!], P 00698808 [image!])).

Note. The epithet 'foliosa' is unavailable in *Goodenia* as it is preoccupied by *Goodenia foliosa* (F.Muell. ex Benth.) Domin (= *G. decursiva* W.Fitzg.).

Etymology. This species commemorates Australian botanists Brendan Lepschi (1969–) and Anna Monro (1974–), in recognition of their tireless service to the botanical community through providing expert nomenclatural and taxonomic advice and maintenance of the *Australian Plant Name Index* (https://biodiversity.org.au/nsl/services/APNI), a truly invaluable resource that lists published Australian vascular plant names and key citations in the literature.

Goodenia capillosa **K.A.Sheph., nom. nov.**

urn:lsid:ipni.org:names:77210080-1

≡ *Velleia hispida* W.Fitzg., *W. Austral. Nat. Hist. Soc.* 1: 25 (1904) – Lectotype (designated by Carolin, Proc. Linn. Soc. New South Wales 92(1): 42 (1967): Nannine, *W.V.Fitzgerald*, Sept. 1903 (NSW 75661, *n.v.*); isolectotype: Australia. Western Australia. Nannine, Sep. 1903, [*W.V.Fitzgerald s.n.*] (PERTH 01639986!)).

Note. The epithet 'hispida' is unavailable in *Goodenia* as it is preoccupied by *G. hispida* R.Br.

Etymology. Named from the Latin *capillosus* (hairy) in reference to the indumentum present on the leaves and sepals.

Goodenia careyi **(F.Muell.) K.A.Sheph. comb. nov.**

urn:lsid:ipni.org:names:77210081-1

≡ *Catospermum careyi* F.Muell., Australas. Chem. Druggist 6: 96. 1884 – Holotype: Australia: Western Australia. Between Northampton and Shark Bay, 1884, *S.Carey s.n.* (MEL 2192442 [image!]). ≡ *Pentaptilon careyi* (F.Muell.) Pritzel, Bot. Jahrb. Syst. 35(4): 564, fig. 65. 1905.

Goodenia caroliniana **K.A.Sheph., nom. nov.**

urn:lsid:ipni.org:names:77210082-1

≡ *Velleia lyrata* R.Br., Prodr. 580. 1810 – Lectotype (designated by Carolin, Proc. Linn. Soc. New South Wales 92(1): 48 (1967): Australia. New South Wales. South Head of Port Jackson, 1803, *R.Brown s.n.* ([Bennett no. 2549] (BM 001041389 [image!]); isolectotypes: BM 001041387 [image!], BM 001041388 [image!], BM 001041390 [image!], CANB 279052!, G-DC 00322630 [image!], K 000215413 [image!]; K 00215414 [image!], K 00215415 [image!], MEL 9713 [image!], P 00698809 [image!], P 00698810 [image!]).

Note. The epithet 'lyrata' is unavailable in *Goodenia* as it is preoccupied by *G. lyrata* Carolin.

Etymology. This species is endemic to the Sydney region of New South Wales and is named in honour of Roger Charles Carolin (1929–), an Associate Professor at the University of Sydney and Curator of the John Ray Herbarium (SYD) for more than 30 years. During his tenure Carolin published numerous treatments including revision of the family Goodeniaceae for the *Flora of Australia*.

Goodenia collaris **(F.Muell.) K.A.Sheph., comb. nov.**

urn:lsid:ipni.org:names:77210083-1

≡ *Scaevola collaris* F.Muell., Rep. pl. Babbage's Exped. 15 (1859) – Type citation: "On sand ridges near Wonnomulla." Possible syntype: Australia. South Australia. Lake Eyre, *s. dat., leg. ign. s.n.* (AD 97604803 [image!]).

Note. Carolin (1992c) cited the type of the name *Scaevola collaris* F.Muell. as "Near Wonnamulla, S.A., *Babbage Expedition*; holo: MEL." A specimen of *S. collaris* labelled "NW interior of South Australia, 1859" (*J.M.Stuart s.n.*, MEL 1520987A, *n.v.*) is held at MEL (N.G. Walsh, pers. comm. 2019), but this is unlikely to represent original material of this name, and Carolin's text may be an interpretation of the type citation rather than label data from any physical specimens. Similarly, a specimen of *S. collaris* at K labelled "Mr McDougal [*sic*; McDouall] Stuart's journey of 1859 to the interior of Australia" (K 000216199 [image!])), is also unlikely to represent original material, as noted by Roger Carolin's 1973 annotation on the specimen. Both specimens at K and MEL are likely to have been collected during McDouall Stuart's second or third expeditions to northern South Australia during 1859, rather than during the Babbage expedition of 1858 (see Morris 1976 and Symes 1969, respectively). A collection at AD (AD 97604803) may represent original material of this name. The collection comprises two flowering branchlets of *Goodenia collaris*, is labelled "Scaevola collaris F.v.Muell. / Lake Eyre" in an unknown hand, and matches the description given in the protologue, with the exception of fruits, which are absent from this material. The AD material is here treated as a possible syntype, in the absence of conclusive information as to its exact origin and history at this time.

Goodenia connata (F.Muell.) K.A.Sheph., comb. nov.

urn:lsid:ipni.org:names:77210084-1

≡ *Velleia connata* F.Muell., Trans. Philos. Soc. Victoria 1: 18. 1855 – Holotype: Australia. Sandhills towards the junction of the Murray & Murrumbidgee, Dec. 1853, *F. von Mueller s.n.* (MEL 594385 [image!]).

Note. Carolin (1967c) cites a Mueller collection at K (K 00215370) as the "Holo (?) type", and states "There is no specimen in MEL corresponding to this and it is assumed the holotype was sent to, and retained by K". Subsequently, Carolin (1992g) treated this same collection as an "iso[type]", and it is annotated by Carolin as "part of the HOLOTYPE." Carolin does not appear to have seen MEL 594385, treated here as the holotype of this name. The MEL specimen is a good match for the protologue, including the locality statement. The specimen at K, referred to and examined by Carolin, represents *Goodenia connata* and is of a similar developmental state as the specimen at MEL. It bears a label in Mueller's hand reading "Velleya (Aceratia) connata FvMueller, Murray Scrub". However, it is not certain whether this specimen is part of the original material, and it is therefore not considered for purposes of typification of this name.

Goodenia cycnopotamica (F.Muell.) K.A.Sheph., comb. nov.

urn:lsid:ipni.org:names:77210085-1

≡ *Velleia cycnopotamica* F.Muell., Fragm. 6: 7. 1867 – Lectotype (designated by Carolin, Proc. Linn. Soc. New South Wales 92(1): 41 (1967): Australia. Western Australia. Without precise locality, *s. dat.*, *J.Drummond 410* (MEL 9798 [image!]; isolectotypes: G 00355707 [image!], P 00689747 [image!], P 00698811 [image!])).

Note. Carolin (1967c) cited the type of the name *Velleia cycnopotamica* F.Muell. as "*Holotype* – Ad flumen cygnorum. Drummond no. 410 (MEL 9798) – *Isotypes* – (P.G)." This is here treated as effective lectotypification by Carolin. As Carolin's citation meets the relevant requirements of ICN Art. 7.11, his use of the terms "holotype" and "isotype" is correctable under ICN Art. 9.10.

Goodenia daviesii (F.Muell.) K.A.Sheph., comb. nov.

urn:lsid:ipni.org:names:77210120-1

≡ *Velleia daviesii* F.Muell., Fragm. 10: 10. 1876 – Holotype: Australia. Western Australia. Near Ularing, 1875, *Young s.n.* (MEL 9647 [image!]).

Goodenia discophora (F.Muell.) K.A.Sheph., comb. nov.
urn:lsid:ipni.org:names:77210086-1

≡ *Velleia discophora* F.Muell., Fragm. 10: 10. 1876 – Holotype: Australia. Western Australia. Near Ularing, 10–15 Oct 1875, *Young s.n.* (MEL 9649 [image!]).

Goodenia etheira K.A.Sheph., nom. nov.
urn:lsid:ipni.org:names:77210087-1

≡ *Verreauxia dyeri* E.Pritz. ex Hemsl., Hooker's Icon. Pl. 28: t. 2782. 1905 – Lectotype (designated by Carolin in A.S.George (ed.), Fl. Austral. 35: 103. 1992: Australia. Western Australia. Railway between Cunderdin and Dedari, 1903, *G.H.Thiselton-Dyer 105* (K 00216471 [image!])).

Note. The epithet 'dyeri' is unavailable in *Goodenia* as it is preoccupied by *Goodenia dyeri* Krause.

Etymology. This species is named for the Greek *etheira* (hair, mane) in reference to the villous hairs on the leaves.

Goodenia exigua F.Muell., Fragm. 3(22): 142. 1863

≡ *Selliera exigua* (F.Muell.) Benth., Fl. Austral. 4: 82. 1868 ≡ *Velleia exigua* (F.Muell.) Carolin in A.S.George (ed.), Fl. Australia 35: 334. 1992 – Lectotype (designated by Carolin in A.S.George (ed.), Fl. Australia. 35: 331. 1992): Australia. Western Australia. Moirs Inlet, *s. dat.*, [*G.Maxwell s.n.*] (MEL 24156 [image!]; isolectotype: K 000216089 [image!]).

Goodenia glabrata (Carolin) K.A.Sheph., comb. nov.
urn:lsid:ipni.org:names:77210088-1

≡ *Velleia glabrata* Carolin, Proc. Linn. Soc. New South Wales 92: 46. 1967 – Holotype: Australia. Queensland. Urimbin, South of Thargomindah, 16 Aug 1964, *R.C.Carolin 4080* (NSW 100797, *n.v.*).

Goodenia heenanii K.A.Sheph., nom. nov.
urn:lsid:ipni.org:names:77210089-1

≡ *Selliera rotundifolia* Heenan, New Zealand J. Bot. 35: 133–137. 1997 – Holotype: New Zealand. Manawatu, Hokio Beach, sand plain behind foredunes, 30 Jan 1996, *P.B.Heenan 4/96* (CHR 507535; isotypes: AK *n.v.*, WELT 81947 [image!]).

Note. The epithet ‘rotundifolia’ is unavailable in *Goodenia* as it is preoccupied by *Goodenia rotundifolia* R.Br.

Etymology. Named in honour of the highly respected New Zealand botanist Peter Heenan (1961–), who first recognised this species as distinct.

Goodenia macrocalyx (de Vriese) K.A.Sheph., comb. nov.

urn:lsid:ipni.org:names:77210090-1

≡ *Velleia macrocalyx* de Vriese, in T.L.Mitchell, J. exped. trop. Australia: 258. 1848 – Holotype: Australia. Sub-Tropical New Holland, 1846, *T.L.Mitchell 237* (L 0001763 [image!]).

Goodenia macrophylla (Lindl.) F.Muell., Fragm. 6(41): 11. 1867

≡ *Euthales macrophylla* Lindl., Edward’s Bot. Reg. 26: 54 (1840)

≡ *Velleia macrophylla* (Lindl.) Benth., Fl. Austral. 4: 47. 1868 – Lectotype (designated by Carolin, Proc. Linn. Soc. New South Wales 92(1): 34 (1967): “(ex) Hort. Soc. Nat. Lond. Grown from seed purchased of James Drummond 1840” (CGE, *n.v.*; isolectotype: K, *n.v.*)).

Goodenia montana (Hook.f.) K.A.Sheph., comb. nov.

urn:lsid:ipni.org:names:77210091-1

≡ *Velleia montana* Hook.f., Hooker’s London J. Bot. 6: 265. 1847 – Lectotype (designated by Carolin, Proc. Linn. Soc. New South Wales 92(1): 56 (1967): Australia. Tasmania. Hampshire Hills, Feb 1837, *R.C.Gunn 227* (K 000215445 [image!])).

Goodenia mystrophylla K.A.Sheph., nom. nov.

urn:lsid:ipni.org:names:77210092-1

≡ *Velleia spathulata* R.Br., Prodr. 580. 1810 – Lectotype (designated by Carolin, Proc. Linn. Soc. New South Wales 92(1): 51 (1967): Australia: New South Wales. … prope Kingstown Newcastle, Oct – Nov 1804, *R.Brown s.n.* (BM 001041385 *p.p.* [image!]); isolectotype: MEL 9776 *p.p.* [image!])).

Note. The epithet ‘spathulata’ is unavailable in *Goodenia* as it is preoccupied by *Goodenia spathulata* de Vriese (= *G. bellidifolia* Sm.).

Etymology. The name is from the Greek *mystron* (spoon) *-phyllus* (-leaved), in reference to its spoon-shaped leaves.

Goodenia panduriformis **(A.Cunn. ex Benth.) K.A.Sheph., comb. nov.**
urn:lsid:ipni.org:names:77210093-1

≡ *Velleia panduriformis* A.Cunn. ex Benth., Fl. Austral. 4: 46. 1868 – Lectotype (first-step designated by Carolin, Proc. Linn. Soc. New South Wales 92(1): 36 (1967): "Goodenough Bay and Point Cunningham, N.W. Coast, A. Cunningham (K)"; second-step (designated here): AUSTRALIA: Western Australia. Point Cunningham & Carlisle Head, the North Point of Goodenough Bay, *s. dat.*, [*A.Cunningham s.n.*] (K 000215368 [image!]; isolectotypes: BM 00104382 [image!], K 000215367 [image!], MEL 9640 [image!])).

Note. Carolin (1967c) designated a collection by Alan Cunningham from "Goodenough Bay and Point Cunningham" at K as the first-step lectotype of *Velleia panduriformis* A.Cunn. ex Benth. The collection designated as lectotype by Carolin comprises two fertile gatherings mounted on one sheet, which have subsequently been treated as two separate accessions with different barcode identifiers. The smaller of these two gatherings (K 000215368), which bears a label in Cunningham's hand, is here chosen as the second-step lectotype.

Goodenia paradoxa **(R.Br.) K.A.Sheph., comb. nov.**
urn:lsid:ipni.org:names:77210094-1

≡ *Velleia paradoxa* R.Br., Prodr. 580. 1810 – Lectotype (designated by Carolin, Proc. Linn. Soc. New South Wales s92(1): 45 (1967): AUSTRALIA. New South Wales. Cow pasture plains, Oct. 1803, *R.Brown s.n.* [Bennett no. 2547] (BM 001041380 (two right-hand specimens only) [image!]; isolectotypes: BM 001041381 [image!], CANB 279053!, K 000215386 [image!],; probable isolectotypes: BM 001041379 (two left-hand specimens only) [image!], BRI AQ225859) [image!], MEL 9866 (left-hand specimens marked 'A' on sheet) [image!], NSW 78419 [image!], P 00698803 [image!])).

Goodenia parvisepta **(Carolin) K.A.Sheph., comb. nov.**
urn:lsid:ipni.org:names:77210095-1

≡ *Velleia parvisepta* Carolin, Proc. Linn. Soc. New South Wales 92: 49. 1967 – Holotype: AUSTRALIA. New South Wales. Dubbo, 8 Nov 1960, *J.Peacock s.n.* (NSW 100660 [image!]).

Goodenia perfoliata **(R.Br.) K.A.Sheph., comb. nov.**
urn:lsid:ipni.org:names:77210096-1

≡ *Velleia perfoliata* R.Br., Prodr. 581. 1810 – Holotype: AUSTRALIA. New South Wales. Blue Mountains, 1803, *A.Gordon s.n.* (BM 001041391 [image!]).

Goodenia radicans **(Cav.) Pers., Syn. pl. 1: 195. 1805**

≡ *Selliera radicans* Cav., Anales Hist. Nat. 1(1): 41, t. 5, fig. 2. 1799 – Type citation: "Crece con abundancia en los húmedos inmediatos al mar de S. Cárlos de Chilow, ... y tambien en el valle distante apenas un a legua de Coquimbo, ... El Sr. Née cogió allí esta planta, que he visto en su herbario, como también el dibuxo que mandó sacar." **Lectotype (designated here)**: Chile. Carlos y Coquimbo [as 'Arica y Coquimbo' on additional, typewritten label (translation of original handwritten label)], *s. dat., L.Née 715* (MA 476260 [image!]. Probable isolectotype: CHILE. In portu Coquimbo … [as 'San Carlos y Coquimbo (Chile)' on additional, typewritten label (translation of original handwritten labels)], *s. dat.*, *L. Née s.n.* (MA 476261 [image!]).

= *Goodenia repens* Labill., Nov. Holl. Pl. 1(5–7): 53, t. 76. 1805 – Type citation: "HABITAT in capite Van-Diemen." **Lectotype (designated here):** … Terra Diemen, *s. dat., J.J.H. Labillardière s.n.* (FI 006937 (ex Herb. Webb) [image!]; probable isolectotypes: FI 006938 [image!]; G-DC 00322613 [image!]; P 00698714 [image!]).

= *Selliera herpystica* Schltdl., Linnaea 20: 598. 1847 – Holotype (*fide* Heuchert et al., Schlentendalia 31: 116. 2017): Australia. South Australia. Südaustralien, auf torfigem im Winter überschwemmten Boden an dem Gawlerriver bei Benthanien, Feb 1845, *H.H.Behr s.n.* (HAL 0098334 [image!]).

= *Selliera microphylla* Colenso, Trans. & Proc. New Zealand Inst. 22: 473. 1889 [1890]. Probable syntypes: New Zealand. Without precise locality, May 1890, *W. Colenso s.n.* (K 000741872 [image!]; New Zealand. Without precise locality, *s. dat.* (WELT 52409 [image!]); New Zealand. Tongariro … 1889, *H.Hill s.n.* (WELT 59062 [image!], WELT 59063 [image!], WELT 59064 [image!]).

Note. *Nee 715* (MA 476260) is here selected as the lectotype of *Selliera radicans* Cav., as it is the most complete of the available syntypes at MA, bearing both flowers and fruit. *Labillardière s.n.* (FI 006937) is here selected as the lectotype of *Goodenia repens* Labill. The specimen is extensively annotated by Labillardiere, and was formerly part of the Philip Webb herbarium (Webb acquired Labillardiere's herbarium in 1834; see Stafleu & Cowan 1979).

Goodenia reinwardtii **(de Vriese) K.A.Sheph., comb. nov.**

urn:lsid:ipni.org:names:77210097-1

≡ *Scaevola reinwardtii* de Vriese in J.G.C.Lehmann, Pl. Preiss. 1(3): 409. 1845 ≡ *Verreauxia reinwardtii* (de Vriese) Benth., Fl. Austral. 4: 105. 1868 – Lectotype (designated by Carolin in A.S.George (ed.), Fl. Austral. 35: 334. 1992): Australia. Western Australia. In planitis arenosa "Quangen" (Victoria), 20 Mar 1840, *L.Preiss* [Plantae Preissianae 1454] (LD 1821186 [image!]; isolectotypes: MEL 42187 [image!], MEL 2192672 [image!]); probable isolectotypes: P 00698676 [image!]), S S08-4783 [image!]).

Goodenia rosea (S.Moore) K.A.Sheph., comb. nov.
urn:lsid:ipni.org:names:77210098-1

≡ *Velleia rosea* S.Moore, J. Linn. Soc. Bot. 34: 202. 1898 – Holotype: Australia. Western Australia. Creek between Wilson's Pool and Lake Darlot, Apr. 1895, *S. Moore s.n.* (BM 001041378 [image!]).

Goodenia subsolana K.A.Sheph., nom. nov.
urn:lsid:ipni.org:names:77210099-1

≡ *Velleia pubescens* R.Br., Prodr. 581. 1810 – Syntypes: Australia. Queensland. Shoalwater Bay and Broad Sound, *s. dat.*, [*R.Brown s.n.*] (BM 001041383 [image!], BM 001041384 [image!], CANB 279054!, K 000215429 [image!], (K 000215430 [image!]), MEL 9796) [image!], P 00698800 [image!].

Note. The epithet 'pubescens' is unavailable in *Goodenia* as it is preoccupied by *Goodenia pubescens* Sieber ex Spreng. (= *Scaevola albida* (Sm.) Druce).

Carolin (1992g) lists two syntypes at BM as the 'lectotype' for *Velliea pubescens* R.Br. and reports lectotypification as having been effected in his 1967 treatment of the genus *Velleia*, viz: "Shoalwater Bay, and Thirsty Sound, [Qld], *R. Brown 87*; lecto: BM, *fide* R.C.Carolin, *Proc. Linn. Soc. New South Wales* 92: 53 (1963) [*sic*; 1967]; isolecto: MEL, P." However, Carolin (1967c, 1992g) does not effectively lectotypify *Velleia pubescens* as he does not clearly indicate the type element by direct citation, as required by ICN Art. 7.11, rather citing two syntype specimens at BM. The gatherings referred to by Carolin (1967c, 1992g) comprise three flowering plants, mounted on one sheet (BM 001041383), and, as noted by Carolin (1967c), Brown's original labels, formerly affixed to the specimens themselves, have been detached and glued to the sheet, thereby making it impossible to determine which specimen relates to which label. A lectotype has not been designated for *Velleia pubescens* R.Br., as this will be effected by D.J.Mabberley in a forthcoming publication on the life and work of Robert Brown (D.J.Mabberley pers. comm. 2020).

Etymology. This species is named for the Latin *subsolanus* (eastern, oriental) as this species is found near coastal habitats of Queensland in eastern Australia.

Goodenia trinervis (Labill.) K.A.Sheph., comb. nov.
urn:lsid:ipni.org:names:77210100-1

≡ *Velleia trinervis* Labill. Nov. Holl. Pl. 1(5–7): 54, t. 77. 1805 – Lectotype (designated by Carolin, Proc. Linn. Soc. New South Wales 92(1): 31. 1967: Australia. Tasmania. Nouvelle Hollande, Côte S. O., *s. dat., J.J.H.Labillardiere s.n.* (P 00698795 (ex Herb. Webb) [image!]; probable isolectotypes: BM 001041376 [image!], B-W 04026 [image!], FI 113248 [image!], G 00355635 [image!], G-DC 00322623 [image!], MEL 9651 [image!], P 00698794 [image!], P 00698796 [image!])).

Goodenia verreauxii **(de Vriese) K.A.Sheph., comb. nov.**

urn:lsid:ipni.org:names:77210101-1

≡ *Dampiera verreauxii* de Vriese, Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2, 10: 118, t. 20. 1854 ≡ *Verreauxia paniculata* Benth., Fl. Austral. 4: 105. 1868, *nom. illeg., nom. superfl.* ≡ *Verreauxia verreauxii* (de Vriese) Carolin, Telopea 2(1): 75. 1980. Type citation: "Nov. Holl. specimine mihi humanissime oblato cum mutlis aliis plantis Novae Hollandiae, a Celeb. Inventore Verreaux, dum hoc. anno 1850 in nostre urbe degebat. Plurimas etiam alias stirpes ab hoc Naturae Investigore repertas et ad Goodenovieas reletas, vidi in Herb. Musei Horti Parisiensis."

Lectotype (here designated). "Dampiera verreauxii" in de Vriese, Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2, 10: t. 20. (1854).

Note. No specimens are cited by de Vriese (1854) in the protologue for *Dampiera verreauxii*, although de Vriese indicates that he examined material of this taxon made available by Verreaux at the Muséum National d'Histoire Naturelle in Paris (P) in 1850. Verreaux visited Australia during 1842–1846 but his collecting efforts were confined to Tasmania and the east coast of Australia (George 2009) and so it is unlikely he would have obtained material from Western Australia directly. Carolin (1992i) postulated that "The type was probably collected by J. Drummond (*Drummond* 4: 186 cited by Krause, loc. cit. [= Pflanzenr. 54: 170 (1912)])". This is possible, as Drummond did collect extensively through south-west Western Australia (including the region where this species occurs) and his specimens were sent to various institutions throughout Australia and Europe. Three Drummond collections of this taxon have been located (MEL 42188 [image!], P 03035588 [image!] and P 04057856 [image!]). However, it is not clear whether these specimens represent original material and neither specimen at P is an exact match for the plant illustrated in the protologue. Accordingly, the illustration included in the protologue is here designated as the lectotype for *Dampiera verreauxii* de Vriese.

Scaevola filifolia **(R.Br.) K.A.Sheph., comb. nov.**

urn:lsid:ipni.org:names:77210372-1

≡ *Diaspasis filifolia* R.Br., Prodr. 587. 1810. *Type citation*: "(M.) v.v." Syntypes: Australia. Western Australia. King George III's Sound, 21 Dec 1801, *R. Brown s.n.* [Bennett No. 2659] (BM 001041412 [image!], BM 001041413 [image!]; K 000216450 [image!]; K 000216453 [image!]; P 00698693 [image!])).

= *Goodenia glandulifera* de Vriese, Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2, 10: 129. 1854 – Lectotype (designated by Carolin, Telopea, 3(4): 566 (1990): Australia. Western Australia. In solo turfoso inter frutices prope urbiculam "Albany" (Plantagenet), 4 Oct. 1840, *L.Preiss s.n.* [Plantae Preissiana 2032] (LD 1677627 [image!]; isolectotype: L 0012072 [image!]).

= *Scaevola clandestina* F.Muell., Fragm. 1(9): 206. 1859 – Type citation: "In Nova Hollandia austro-occidentali." Type: *n.v.*

Note. A lectotype has not been designated for *Diaspasis filifolia* R.Br., as this will be effected by D.J.Mabberley in a forthcoming publication on the life and work of Robert Brown (D.J.Mabberley pers. comm. 2020).

Acknowledgements

The authors gratefully acknowledge the following institutes for supporting visits to examine specimens and allow tissue sampling (AD, BRI, CANB, DNA, MEL, NSW) and the curation team at PERTH for facilitating loans and providing unfailing support to KAS throughout this study. KAS was also a grateful recipient of a Winston Churchill Memorial Trust Fellowship, sponsored by the Australian Biological Resources Study, that facilitated travel to Europe to examine specimens lodged at BM, CGE, K, LD and W, and these institutions are also gratefully acknowledged. Thanks go to Ailsa Holland and Paul Forster (BRI), Neville Walsh (MEL), David Albrecht (CANB), Ian Cowie (DNA), Peter Lang (AD) and Peter Heenan for helpful discussion and the confirmation of identifications and K.R. McDonald (BRI), Bob Chinnock (AD), Matthew Barrett (CNS) and Russell Barrett (NSW) who supplied vouchers for DNA sequencing. Ian Cowie provided information on the Northern Territory collections of *Goodenia* as well as access to the highly informative illustrations of plants and seeds by Monika Osterkamp Madsen for the *Northern Territory Flora*. Sincere thanks also to Juliet Wege and Terry Macfarlane (PERTH), Anna Monro (CANB), Neville Walsh (MEL), Wayne Gebert (MEL), David Mabberley (Sydney), Helen Vonow (AD) and Russell Barrett (NSW) for their sound advice in navigating nomenclatural conundrums and for providing information on type material and historical collections. Particular thanks are due to Robyn Barker (AD) for her considered assistance in interpreting original material of *Scaevola collaris*. Field support was ably provided by Spencer Willis, Juliet Wege, Carol Wilkins and others. Wendy Thompson diligently examined specimens to confirm inflorescence characters included in Table 2 while the following people are acknowledged for allowing the use of their images: Kevin Thiele, Rob Davis, Fred & Jean Hort, Craig Nieminski, Russell Barrett, Andrew Perkins, Andrew Crawford, N. Blair, R. Fryer, J. Newland, J. Tann, R. Cumming and Seeds of South Australia (https://spapps.environment.sa.gov.au/seedsofsa/). US National Science Foundation grant DEB no. 125-6946 provided funding support for earlier aspects of this work. David Albrecht is thanked for providing helpful comments on an earlier draft, as are the reviewers Laura Lagomarsino, Dianella Howarth and

Russell Barrett, and associate editor Clifford Morden. We would also like to finally thank our families, friends and past students for their support. This study is the culmination of many years of research by an international collaboration on a predominantly Australian plant group, as such we acknowledge the Traditional Custodians of the lands on which these plants grow and pay our sincere respects to their Elders past, present and emerging.

References

Albrecht DE (2002) New species and notes on central Australian *Goodenia* (Goodeniaceae). Nuytsia 15(1): 1–9.

Applequist WL (2019) Report of the Nomenclature Committee for Vascular Plants: 70. Taxon 68(4): 847–854. https://doi.org/10.1002/tax.12113

Barrett RL, Barrett MD (2014) Four new species of Goodeniaceae from Western Australia, including the smallest species in the family, a putative seed-article elaiosome and possible floral mimicry in *Lechenaultia*. Australian Systematic Botany 27(6): 469–482. https://doi.org/10.1071/SB14035

Barrett RL, Barrett MD (2018) Reinstatement of *Goodenia pritzelii* Domin (Goodeniaceae) from the north Kimberley and description of *G. oenpelliensis* as a new species from the Northern Territory. Telopea 21: 9–17.

Briggs BG, Johnson LAS (1979) Evolution in the Myrtaceae – evidence from inflorescence structure. Proceedings of the Linnean Society of New South Wales 102: 157–256.

Brown R (1810) Prodromus florae Novae Hollandiae et insulae Van-Diemen, exhibens characteres plantarum quas annis 1802–1805: 586–587. Taylor & Socii, Londini. https://doi.org/10.5962/bhl.title.3678

Carolin RC (1959) Floral structure and anatomy of the Family Goodeniaceae Dumort. Proceedings of the Linnean Society of New South Wales 84: 242–255.

Carolin RC (1960) The structures involved in the presentation of pollen to visiting insects in the order Campanulales. Proceedings of the Linnean Society of New South Wales 85: 197–207.

Carolin RC (1966) Seeds and fruit of the Goodeniaceae. Proceedings of the Linnean Society of New South Wales 91: 58–83.

Carolin RC (1967a) The concept of the inflorescence in the order Campanulales. Proceedings of the Linnean Society of New South Wales 92: 7–26.

Carolin RC (1967b) *Coopernookia*: A new genus of Goodeniaceae. Proceedings of the Linnean Society of New South Wales 92: 209–216.

Carolin RC (1967c) The genus *Velleia*. Proceedings of the Linnean Society of New South Wales 92: 27–57.

Carolin RC (1971) The trichomes of the Goodeniaceae. Proceedings of the Linnean Society of New South Wales 96: 8–22.

Carolin RC (1977) The systematic relationships of *Brunonia*. Brunonia 1(1): 9–29. https://doi.org/10.1071/BRU9780009

Carolin RC (1980) Pattern of the seed surface of *Goodenia* and related genera. Australian Journal of Botany 28(1): 123–137. https://doi.org/10.1071/BT9800123

Carolin RC (1990) Nomenclatural notes and new taxa in the genus *Goodenia* (Goodeniaceae). Telopea 3(4): 517–570. https://doi.org/10.7751/telopea19904905

Carolin RC (1992a) Brunoniaceae. In: George AS (Ed.) Flora of Australia vol. 35. Australian Government Publishing Service, Canberra, 1–3.

Carolin RC (1992b) *Coopernookia*. In: George AS (Ed.) Flora of Australia vol. 35. Australian Government Publishing Service, Canberra, 80–84.

Carolin RC (1992c) *Scaevola*. In: George AS (Ed.) Flora of Australia vol. 35. Australian Government Publishing Service, Canberra, 84–146.

Carolin RC (1992d) *Diaspasis*. In: George AS (Ed.) Flora of Australia vol. 35. Australian Government Publishing Service, Canberra, 146–147.

Carolin RC (1992e) *Goodenia*. In: George AS (Ed.) Flora of Australia vol. 35. Australian Government Publishing Service, Canberra, 147–281.

Carolin RC (1992f) *Selliera*. In: George AS (Ed.) Flora of Australia vol. 35. Australian Government Publishing Service, Canberra, 281–282.

Carolin RC (1992g) *Velleia*. In: George AS (Ed.) Flora of Australia vol. 35. Australian Government Publishing Service, Canberra, 282–297.

Carolin RC (1992h) *Pentaptilon*. In: George AS (Ed.) Flora of Australia vol. 35. Australian Government Publishing Service, Canberra, 297.

Carolin RC (1992i) *Verreauxia*. In: George AS (Ed.) Flora of Australia vol. 35. Australian Government Publishing Service, Canberra, 298–300.

Carolin RC (2007) Goodeniaceae. In: Kadereit JW, Jeffrey C (Eds) The Families and Genera of Vascular Plants Vol. VIII: Asterales. Springer, 589–590. https://doi.org/10.1007/978-3-540-31051-8_8

Carolin RC, Rajput MTM, Morrison D (1992) Goodeniaceae. In: George AS (Ed.) Flora of Australia vol. 35. Australian Government Publishing Service, Canberra, 4–351.

Council of Heads of Australasian Herbaria (2006-) National Species List. https://biodiversity.org.au/nsl/services/APC [accessed 14 August 2018]

Cowie ID (2005) *Goodenia elaiosoma* I.D.Cowie (Goodeniaceae), a new species from the Top End of the Northern Territory and a key to the northern species. Austrobaileya 7(1): 205–213.

Cranfield RJ, Sage LW (1997) *Goodenia katabudjar* (Goodeniaceae), a new species from southwest Western Australia. Nuytsia 11(3): 297–299.

Cronquist A (1981) An integrated system of classification of flowering plants. Columbia University Press, New York.

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: More models, new heuristics and parallel computing. Nature Methods 9(8): 772. https://doi.org/10.1038/nmeth.2109

Don G (1834) A General History of Dichlamydeous Plants. 3: 725. JG, F Rivington, London.

Gardner CA, George AS (1963) Eight new plants from Western Australia. Journal of the Royal Society of Western Australia 46: 137–138.

Gardner AG, Sessa EB, Michener P, Johnson E, Shepherd KA, Howarth DG, Jabaily RS (2016a) Utilizing next-generation sequencing to resolve the backbone of the Core Goodeniaceae and inform future taxonomic and floral form studies. Molecular Phylogenetics and Evolution 94: 605–617. https://doi.org/10.1016/j.ympev.2015.10.003

Gardner AG, Fitzgerald JN, Menz J, Shepherd KA, Howarth DG, Jabaily RS (2016b) Characterizing floral symmetry in the Core Goodeniaceae with geometric morphometrics. PLoS One 11(5): e0154736. https://doi.org/10.1371/journal.pone.0154736

George AS (2009) Australian botanist's companion. Four Gables Press, Kardinya, Western Australia.

Gibson N (2014) An amphibious *Goodenia* (Goodeniaceae) from an ephemeral arid zone wetland. Nuytsia 24: 23–28.

Guindon S, Gascuel O (2003) A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Systematic Biology 52(5): 696–704. https://doi.org/10.1080/10635150390235520

Gustafsson MHG, Backlund A, Bremer B (1996) Phylogeny of the Asterales sensu lato based on rbcL sequences with particular reference to the Goodeniaceae. Plant Systematics and Evolution 199(3–4): 217–242. https://doi.org/10.1007/BF00984906

Holland AE (2015) *Goodenia effusa* (Goodeniaceae), a new species from north Queensland, Australia. Telopea 18: 61–65. https://doi.org/10.7751/telopea8469

Holland AE, Boyle TP (2002) Four new species of *Goodenia* Smith (Goodeniaceae) from Queensland. Austrobaileya 6: 253–265.

Hong D, Howarth DG (2011) Goodeniaceae. In: Zheng-yi W, Raven PH, Hong D (Eds) Flora of China. Cucurbitaceae through Valerianaceae, with Annonaceae and Berberidaceae, vol. 19. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 569.

Howarth DG, Baum DA (2005) Genealogical evidence of homoploid hybrid speciation in an adaptive radiation of *Scaevola* (Goodeniaceae) in the Hawaiian Islands. Evolution; International Journal of Organic Evolution 59(5): 948–961. https://doi.org/10.1111/j.0014-3820.2005.tb01034.x

Howarth DG, Gustafsson MHG, Baum DA, Motley TJ (2003) Phylogenetics of the genus *Scaevola* (Goodeniaceae): Implications for dispersal patterns across the Pacific Basin and colonization of the Hawaiian Islands. American Journal of Botany 90(6): 915–923. https://doi.org/10.3732/ajb.90.6.915

Jabaily RS, Shepherd KA, Gustafsson MHG, Sage LW, Krauss SL, Howarth DG, Motley TJ (2012) Systematics of the Austral-Pacific family Goodeniaceae: Establishing a taxonomic and evolutionary framework. Taxon 61(2): 419–436. https://doi.org/10.1002/tax.612012

Jabaily RS, Shepherd KA, Gardner AG, Gustafsson MHG, Howarth DG, Motley TJ (2014) Historical biogeography of the predominantly Australian plant family Goodeniaceae. Journal of Biogeography 41(11): 2057–2067. https://doi.org/10.1111/jbi.12363

Jabaily RS, Shepherd KA, Michener PS, Bush CJ, Rivero R, Gardner AG, Sessa EB (2018) Employing hypothesis testing and data from multiple genomic compartments to resolve recalcitrant backbone nodes in *Goodenia s.l.* (Goodeniaceae). Molecular Phylogenetics and Evolution 127: 502–512. https://doi.org/10.1016/j.ympev.2018.05.005

Jeanes JA (1999) Goodeniaceae. In: Walsh NG, Entwisle TJ (Eds) Flora of Victoria Vol. 4, Cornaceae to Asteraceae. Inkata Press, Melbourne.

Kanis A (1981) An introduction to the system of classification used in the Flora of Australia. In: George AS (Ed.) Flora of Australia vol. 1. Australian Government Publishing Service, Canberra, 77–111.

Karthigeyan K, Sumathi R, Jayanthi J, Diwakar PG (2009) New records of plants to the flora of India from South Andaman Island. Indian Journal of Forestry 32: 301–303.

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Mentjies P, Drummond A (2012) Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics (Oxford, England) 28(12): 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Krause K (1912) Goodeniaceae. In: Engler A (Ed.) Das Pflanzenreich., IV. 277 u. 277a. Verlag von Wilhelm Engelmann, Leipzig, 1–207.

Lang PJ (2014) *Goodenia valdentata* (Goodeniaceae), a new rare species endemic to Davenport Range, South Australia. Journal of the Adelaide Botanic Gardens 27: 47–56.

Leenhouts P (1957) Goodeniaceae. In: Steenis CGGJ van (Ed.) Flora Malesiana ser. 1, 5. Nordhoff, Djakata, 335–344.

Miller MA, Pfeiffer W, Schwartz T (2010) "Creating the CIPRES Science Gateway for inference of large phylogenetic trees". Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA, 1–8. https://doi.org/10.1109/GCE.2010.5676129

Morris D (1976) Stuart, John McDouall (1815–1866). In: Serle G (Ed.) Australian Dictionary of Biography, 6, Melbourne University Press, Melbourne, 214–215.

Peacock WJ (1963) Chromosome numbers and cytoevolution in the Goodeniaceae. Proceedings of the Linnean Society of New South Wales 88: 8–27.

Pellow BJ, Porter JL (2005) A new species of *Goodenia* (Goodeniaceae) from Nocoleche Nature Reserve, Far Western Plains, New South Wales. Telopea 11(1): 35–41. https://doi.org/10.7751/telopea20055702

Persoon CH (1805) *Goodenia*. Synopsis plantarum 1: 195. CF Cramerum, Parisiis Lutetiorum.

Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1.6. http://beast.bio.ed.ac.uk/Tracer

Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 31(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Sage LW (2000) New taxa in *Goodenia* (Goodeniaceae) from the south-west of Western Australia, with an update to the *Goodenia* key in the 'Flora of Australia'. Nuytsia 13: 367–377.

Sage LW (2001) New taxa in *Goodenia* (Goodeniaceae) from the Kimberley region of Western Australia. Nuytsia 13: 529–536.

Sage LW, Albrecht DE (2006) New taxa in *Goodenia* subgenus *Goodenia* section *Caeruleae* subsection *Scaevolina* (Goodeniaceae), from the Eremaean Botanical Province of Western Australia. Nuytsia 16: 167–174.

Sage LW, Dixon KW (2005) *Goodenia pedicellata* (Goodeniaceae), a new species from the Pilbara bioregion of Western Australia. Nuytsia 15: 513–516.

Sage LW, Pigott JP (2003) Conservation status of *Goodenia* (Goodeniaceae) in Western Australia, including a review of threatened, rare and poorly known species. Journal of the Royal Society of Western Australia 86: 123–132.

Sage LW, Shepherd KA (2007) Five new conservation-listed species of *Goodenia* (Goodeniaceae) from southern Western Australia. Nuytsia 17: 331–346.

Shepherd KA, Wege JA, Jabaily RS (2017) (2526) Proposal to conserve the name *Goodenia* (Goodeniaceae) with a conserved type. Taxon 66(3): 757–758. https://doi.org/10.12705/663.25

Smith MG, Jones A (2018) Threatened and Priority Flora list 16 January 2018. Department of Biodiversity, Conservation and Attractions. https://www.dpaw.wa.gov.au/plants-and-animals/threatened-species-and-communities/threatened-plants [accessed 7 August 2018]

Stafleu FA, Cowan RS (1979) Taxonomic Literature, 2nd edn, 2. Bohn, Scheltema & Holkema, Utrecht and dr. W.Junk b.v., The Hague.

Stamatakis A (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics (Oxford, England) 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Symes GW (1969) Babbage, Benjamin Herschel (1815–1878). In: Pike D (Ed.) Australian Dictionary of Biography, 3, Melbourne University Press, Melbourne, 65–66.

Tank DC, Donoghue MJ (2010) Phylogeny and phylogenetic nomenclature of the Campanilidae based on an expanded sample of genes and taxa. Systematic Biology 35: 425–441. https://doi.org/10.1600/036364410791638306

Vriese WH de (1854) Goodenovieae. Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem ser. 2, 10.

Wege JA, Shepherd KA, Butcher R, Macfarlane TD, Coates DJ, Thiele KR (2015) Strategic taxonomy in a biodiverse landscape: A novel approach to maximizing conservation outcomes for rare and poorly known flora. Biodiversity and Conservation 24(1): 17–32. https://doi.org/10.1007/s10531-014-0785-4

Western Australian Herbarium (1998-) FloraBase-the Western Australian Flora. Department of Biodiversity, Conservation and Attractions. https://florabase.dpaw.wa.gov.au/ [accessed 7 August 2018]

Supplementary material 1

Summary of GenBank accession numbers, Taxon names, Project numbers, Herbarium Accession numbers, voucher collectors and collection numbers, phylogenetic position and taxonomy and classification according to Shepherd et al.

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: species data

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl1

Supplementary material 2

Goodenia Clade A cpDNA (trnL-F, matK) phylogeny

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: PDF File

Explanation note: Phylogeny of concatenated chloroplast loci trnL-F and matK for *Goodenia* Clade A

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl2

Supplementary material 3

***Goodenia* Clade A nrITS phylogeny**

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: PDF File

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl3

Supplementary material 4

***Goodenia* Clade B cpDNA (trnL-F, matK) phylogeny**

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: PDF File

Explanation note: Phylogeny of concatenated chloroplast loci trnL-F and matK for *Goodenia* Clade B

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl4

Supplementary material 5

Goodenia Clade B nrITS phylogeny

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: PDF File

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl5

Supplementary material 6

Goodenia Clade C cpDNA (trnL-F, matK) phylogeny

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: PDF File

Explanation note: Phylogeny of concatenated chloroplast loci trnL-F and matK for *Goodenia* Clade C

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl6

Supplementary material 7

Goodenia Clade C nrITS phylogeny

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: PDF File

Explanation note: Phylogeny of nrITS for *Goodenia* Clade C

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl7

Supplementary material 8

Goodenia Clade A cpDNA (trnL-F, matK) alignment

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: Nexus formatted alignment

Explanation note: Alignment of concatenated chloroplast loci trnL-F and matK for *Goodenia* Clade A

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl8

Supplementary material 9

Goodenia Clade A nrITS alignment

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: Nexus formatted alignment

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl9

Supplementary material 10

Goodenia Clade B cpDNA (trnL-F, matK) alignment

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: Nexus formatted alignment

Explanation note: Alignment of concatenated chloroplast loci trnL-F and matK for *Goodenia* Clade B

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl10

Supplementary material 11

Goodenia Clade B nrITS alignment

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: Nexus formatted alignment

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl11

Supplementary material 12

Goodenia Clade C cpDNA (trnL-F, matK) alignment

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: Nexus formatted alignment

Explanation note: Alignment of concatenated chloroplast loci trnL-F and matK for *Goodenia* Clade C

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl12

Supplementary material 13

Goodenia Clade C nrITS alignment

Authors: Kelly A. Shepherd, Brendan J. Lepschi, Eden A. Johnson, Andrew G. Gardner, Emily B. Sessa and Rachel S. Jabaily

Data type: Nexus formatted alignment

Link: https://doi.org/10.3897/phytokeys.152.49604.suppl13

PhytoKeys 152: 105–110 (2020)
doi: 10.3897/phytokeys.152.51494
http://phytokeys.pensoft.net

SHORT COMMUNICATION

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Lectotypification of *Abies fanjingshanensis* (Pinaceae)

Yong Yang[1], Keith Rushforth[2]

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Academic editor: D. Stevenson | Received 26 February 2020 | Accepted 28 May 2020 | Published 7 July 2020

Citation: Yang Y, Rushforth K (2020) Lectotypification of *Abies fanjingshanensis* (Pinaceae). PhytoKeys 152: 105–110. https://doi.org/10.3897/phytokeys.152.51494

Abstract

The type collection of *Abies fanjingshanensis* W.L.Huang et al. contains four specimens in the Herbarium (GNUG). *Abies fanjingshanensis* is lectotypified here with *L.Yang 83-427* (GNUG0002022) under Art. 9.12 of the *Shenzhen Code*.

Keywords

Abies fanjingshanensis, China, gymnosperms, lectotypification, *Shenzhen Code*

Introduction

Abies fanjingshanensis W.L.Huang et al. of the Pinaceae is endemic to Fanjing Shan of Guizhou of south-western China (Huang et al. 1984; Fu et al. 1999). The type of the specific name is not clearly indicated. Huang et al. (1984) designated *L.Yang 83-427* (GNUG) as the type in the protologue. We found four specimens with the same collection number in GNUG, two of them [GNUG0002022 (Fig. 1) and GNUG0002122] are marked with "*L.Yang* (杨龙)" as the collector, the third one (GNUG0002123, Fig. 2) is marked with "*Y.L.Tu* (屠玉麟)" as the collector and the fourth one (GNUG0000428, Fig. 3) has no collector. All four specimens were identified as *Abies fanjingshanensis* and they match the characters of the species. It is reasonable to consider that *L.Yang* and *Y.L.Tu* are two collectors of a team because all four specimens were collected from the same locality *Fanjing Shan* on the same day 2 Nov 1983 and the two collectors are also the co-authors of the paper describing the new


贵阳师范学院地理系植物标本

采集記录

标本号数

采集号数 83-427

地点：梵净山大烂茶顶 海拔高 2300m 公尺

采集日期 1983 年 11 月 2 日

采集人 杨龙

环境：

性状：

分布：

形态：

树皮：

叶：

花：

果：

用途：

土名：梵净山冷杉

附记：

学名：Abies fanjingshanensis 科 松科

鉴定人：杨龙

No.83-427 1983年11月2日

贵州 梵净山大烂茶顶

2300米

梵净山冷杉

Abies fanjingshanensis Huang, Tu et Fang

鉴定人 日期

贵州师范大学地理与环境科学学院植物标本室 (GNUG)

GNUG 0002022

Figure 1. Lectotype of *Abies fanjingshanensis* (GNUG0002022), labelled with "*L. Yang* (杨龙)" as the collector.

Figure 2. Isolectotype of *Abies fanjingshanensis* (GNUG0002123), labelled with "*Y.L. Tu* (屠玉麟)" as the collector.

Figure 3. Isolectotype of (GNUG0000428), no collector is indicated on the collection label.

species. They may have collected the specimens together and gave the same number of the collection *83-427*, though they wrote different collector names on the collection notes. None of the four specimens is marked with "type" or equivalent words in Chinese. As a result, the type of *Abies fanjingshanensis* is not clearly indicated according to the existing original materials and we consider that the four specimens are the syntypes (Art. 9.5, Turland et al. 2018). Amongst the four specimens, two specimens are preserved with vegetative shoots having one or a few detached seed scales; one specimen (GNUG0000428) is a reproductive shoot having partially disintegrated female cones; and one specimen (GNUG0002022) is well preserved with a reproductive shoot having a good female cone. Thus GNUG0002022 is the most representative specimen and is one of the two annotated *L.Yang 83-427*. Accordingly, we designate it as the lectotype of *Abies fanjingshanensis* here under Art. 9.12 (Turland et al. 2018).

Typification

***Abies fanjingshanensis* W.L.Huang et al., Acta Phytotax. Sin. 22(2): 154 (1984)**

≡ *Abies fargesii* var. *fanjingshanensis* (W.L.Huang et al.) Silba, Phytologia 68(1): 15 (1990).

Type. China. Guizhou (贵州): Jiangkou (江口), Fanjing Shan (梵净山), northern slope along mountain ridge, alt. 2300 m, 2 Nov 1983, *L.Yang* (杨龙) *83-427* (lectotype, designated here: GNUG0002022; isolectotypes: GNUG0000428, GNUG0002123, GNUG0002122, PE00000459).

Note. We found one specimen photo of the type collection *L.Yang 83-427* (PE00000459) in the Herbarium PE identified as *Abies fanjingshanensis* and labelled with "Isotypus" by L.K.Fu on 31 Jan 1989. We consider this specimen as the isolectotype.

Acknowledgements

Images of the type collection of *Abies fanjingshanensis* were obtained from the Chinese Virtual Herbarium (CVH, http://www.cvh.ac.cn/). This work was supported by the National Natural Science Foundation of China [31970205 & 31770211].

References

Fu LG, Li N, Elias TS (1999) *Abies* Miller, Gard. Dict., Abr. ed. 4, 1: [11]. 1754. In: Wu CY, Raven PR (Eds) Flora of China (Vol. 4). Science Press, Beijing & Missouri Botanical Garden, St. Louis, 44–52.

Huang WL, Tu YL, Yang L (1984) A new species of *Abies* Mill. – *Abies fanjingshanensis.* Acta Phytotaxonomica Sinica 22(2): 154–155.

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber WH, Li DZ, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF [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. Koeltz Botanical Books, Glashütten. https://doi.org/10.12705/Code.2018

PhytoKeys 152: 111–120 (2020)
doi: 10.3897/phytokeys.152.50968
http://phytokeys.pensoft.net

RESEARCH ARTICLE

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Primulina hochiensis var. *ochroleuca* (Gesneriaceae), a new variety from a limestone area of Guangxi, China, and errata on five new species of *Primulina*

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Academic editor: E. Fischer | Received 10 February 2020 | Accepted 28 May 2020 | Published 7 July 2020

Citation: Ge Y-Z, Xin Z-B, Fu L-F, Chou W-C, Huang Y, Huang Z-J, Maciejewski S, Wen F (2020) *Primulina hochiensis* var. *ochroleuca* (Gesneriaceae), a new variety from a limestone area of Guangxi, China, and errata on five new species of *Primulina*. PhytoKeys 152: 111–120. https://doi.org/10.3897/phytokeys.152.50968

Abstract

Primulina hochiensis var. *ochroleuca*, a new variety from a limestone hill of karst areas, Guangxi, China is described with color photographs. It resembles *P. hochiensis* var. *hochiensis*, *P. hochiensis* var. *ovata* and *P. hochiensis* var. *rosulata*, but can be easily distinguished by a combination of characteristics, especially by its corolla color. We found only one population with approx. 3000 mature individuals at the type locality. This variety is provisionally assessed as vulnerable [VU C1] using IUCN criteria.

Keywords

Cliff-dwelling, flora of Guangxi, limestone flora, taxonomy

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* Contributed equally as the first authors.

Introduction

By the end of December 2019, the genus *Primulina* Hance (1883) comprised over 220 species names (infraspecific taxa included) (Wen et al. 2019, 2020; IPNI 2020; Tropicos 2020), including many new species published in recent years (e.g., Pan et al. 2020). In all taxa of *Primulina* in the world at present, 208 were recorded from China and 21 were recorded from Vietnam (Vu 2018; Wen et al. 2020). As the largest genus of Gesneriaceae in China, *Primulina* s. l. has become representative of the rich diversity in the Chinese Gesneriaceae. Nevertheless, it is still possible to dig deeper into the biodiversity of *Primulina* (Möller 2019). Those highly diverse taxa mainly grow in limestone areas, which are highly fragmented and heterogeneous (Möller et al. 2016). Most species are micro-endemics with narrow, island-like distributions, often limited to a single cave or karst limestone hill system (Kang et al. 2014). This edaphic complexity may be a strong driver of speciation via habitat specialization (local adaptations) to edaphic microhabitats (Hao et al. 2015). In addition, Kong et al. (2017) suggest that global temperature change is probably the primary driver of diversification in *Primulina*. And the monsoons and edaphic characteristics are probably also strongly linked to its diversification.

Primulina hochiensis was first published as *Chirita hochiensis* C.C. Huang & X.X. Chen (1992). According to the results of molecular phylogenetic studies, almost all species of *Chirita* sect. *Gibbosaccus* C.B. Clarke, 1883 were merged into *Primulina* Hance (Wang et al. 2011; Weber et al. 2011), including *C. hochiensis*, which was revised as *P. hochiensis* (C.C. Huang & X.X. Chen) Mich. Möller and A. Weber. *Primulina hochiensis* var. *rosulata* F. Wen & Y.G. Wei from Guangxi, China was published as a variety (Wen et al. 2012), and was raised to the rank of species based on its phylogenetic distance from *P. hochiensis* and *P. yingdeensis* Z.L. Ning, M. Kang & X.Y. Zhuang (Ning et al. 2016), but was demoted again as a variety, after performing further population genetical analyses (Yang 2018; Yang et al. 2019). Meanwhile, *P. tsoongii* H.L. Liang, Bo Zhao & Fang Wen (Liang et al. 2013) was treated as a synonym of *P. hochiensis* var. *rosulata*, and another new variety, *P. hochiensis* var. *ovata* L.H. Yang, H.H. Kong & M. Kang, was confirmed and published (Yang et al. 2019).

Two amateurs of Gesneriaceae from Guangxi found this unknown taxon in the wild in late September 2017. The population was not in flowering at that time, only the white buds that were about to bloom. They thought it might be a member of *P. hochiensis* complex because its habit resembles *P. hochiensis* var. *hochiensis* and *P. hochiensis* var. *rosulata*, but differs from the former by its stolon absent, and from the latter by its conspicuously larger leaf blade and longer pedicel. Although it was thought to be *P. hochiensis*, some individuals were collected for cultivation. When all the individuals are in flower, they found that all the flowers are yellow and the color is very stable, hence it can be distinguished from all the other varieties by this character. They visited the original locality again in late October 2017 and found all the individuals' flowers are yellow. Some living plants were collected and mailed to GCCC for further study. We grew them in common garden of GCCC with other varieties of *P. hochiensis* for two years and found that all the flowers of this unknown taxon are yellow, and can be distinguished from all the other varieties. And we made an extensive survey of the surrounding hills in October 2019 when this unknown taxon was in flower. No individual of this unknown taxon was found in the surrounding limestone hills, only some *P. hochiensis* var. *ovata* growing on those hills. Though the distribution of this new variety is close to *P. hochiensis* var. *ovata*, we can easily tell them apart.

After analyzing the morphological characters on these plants, and comparing them with the other three similar-looking *P. hochiensis* varieties, we confirmed that it is indeed a new variety of *P. hochiensis*. Thus, we describe it here.

Taxonomic treatment

***Primulina hochiensis* (C.C.Huang & X.X.Chen) Mich.Möller & A.Weber var. *ochroleuca* F.Wen, Y.Z.Ge & Z.B.Xin, var. nov.**

urn:lsid:ipni.org:names:77210102-1

Figs 1, 2A

Diagnosis. The new variety can be easily distinguished from all varieties of *Primulina hochiensis* by its pale yellow corolla. It differs from the typical variety, *P. hochiensis* var. *hochiensis* by its stolon lacking and obviously longer petiole (5–7 cm long); from *P. hochiensis* var. *ovata* by its stolon lacking, obviously longer petiole (5–7 cm long) and longer pedicel (1.5–2 cm long); from *P. hochiensis* var. *rosulata* by its longer pedicel (1.5–2 cm long), shorter calyx (3.5–4 mm long), corolla throat with one big yellow patch and longer pistil (1.4–1.8 cm long).

Type. China. Guangxi Zhuang Autonomous Region, Guilin City, Gongcheng County, Xiling Town, 24°55'N, 110°45'E, altitude ca. 220 m, 8 October 2019, *Fang Wen et al.*, *WF191008-03* (Holotype: IBK!; Isotypes: IBK!).

Description. Herbs perennial, acaulescent. Leaves basal, 20–35; petiole cylindrical, densely extremely short pubescent, 5–7 × 0.4–0.5 cm; leaf blade elliptical to slightly ovate, 5.5–7.5 (–9) × 3–5 cm, densely appressed puberulent, base cuneate, margin entire, apex acute; lateral veins 4–6 on each side of the midrib, conspicuous on the abaxial surface, inconspicuous on the adaxial surface. Cymes 4–6, axillary, 1–3-branched, 2–8-flowered; peduncle 5–10 cm long, 1–1.5 mm in diameter, densely erect puberulent; bracts 2, opposite, linear, 3–3.5 × 1 mm, puberulent. Pedicel 1.5–2 cm long, 1–1.5 mm in diameter, puberulent. Calyx 5-parted from the base; segments equal, lanceolate-linear, 3.5–4 × 1–1.2 mm, densely pubescent, margin entire, apex acute. Corolla pale yellow, throat with two distinctly elliptic yellow spots, 2.5–3 cm long, orifice 0.6–0.8 cm in diameter, outside puberulent with both glandular and eglandular hairs, inside glabrous; tube narrowly infundibuliform, 1–1.2 cm long; limb distinctly 2-lipped, adaxial lip 2-parted to the base, lobes slightly oblique linguiform or ovate, ca. 5 × 2.5 mm; abaxial lip 3-parted to the middle, lobes obliquely ovate, ca. 8 × 4 mm. Stamens 2, adnate to ca 1.0 cm above the corolla base; anthers purple, reniform, ca. 1.5 × 1.2 mm, slightly constricted at the middle; filaments geniculate close to the base, ca. 6 mm long, glabrous; staminodes 3, lateral ones short linear, glabrous, 1–1.2 mm long, adnate to

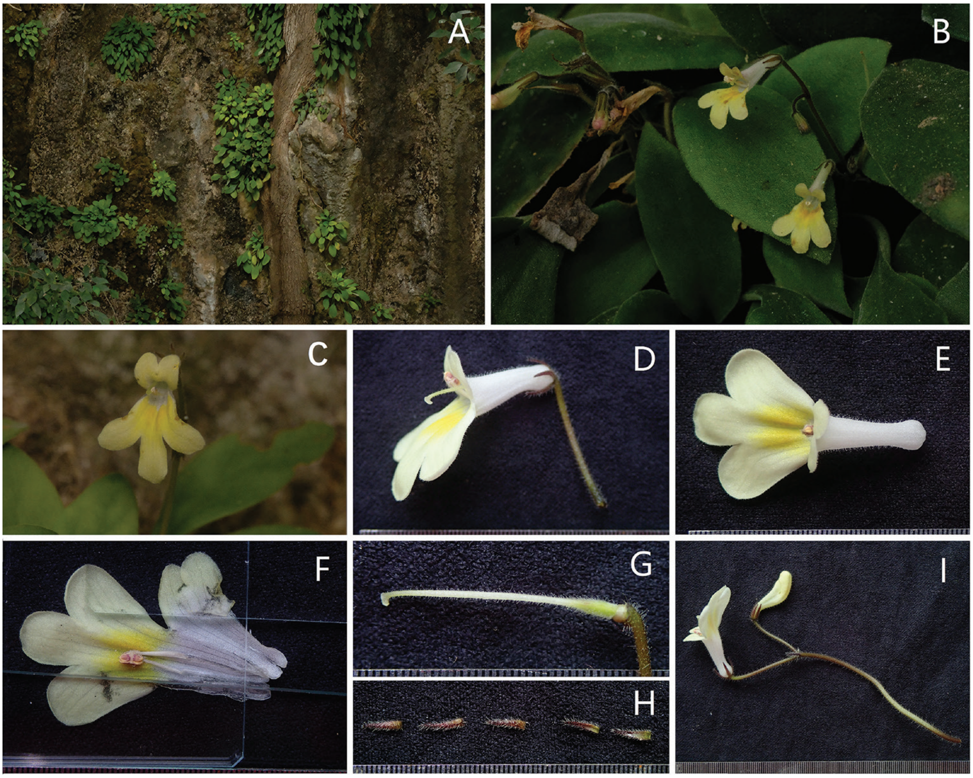

Figure 1. *Primulina hochiensis* var. *ochroleuca* **A** habitat **B** habit **C** frontal view of corolla **D** lateral view of corolla **E** top view of corolla **F** opened corolla with stamens and staminodes **G** pistil **H** calyx lobes **I** cyme with flowers (Photographed by Fang Wen).

4–5 mm above the corolla base, the central one linear, 0.8–1 mm long, adnate to 2.5–3 mm above the corolla base. Disc annular, margin entire or sometimes slightly erose, ca. 0.7 mm high. Pistil 1.4–1.8 cm long; ovary linear, 3–4 mm long, 1–1.5 mm in diameter, densely puberulent with both glandular and eglandular hairs; style 1.1–1.4 cm long, ca. 0.5 mm in diameter, glandular-puberulent. Stigmas translucent to white, obtrapeziform, apex 2-parted up to the middle, 0.8–1 mm long. Capsule linear, 1.8–2 cm long, ca. 1.5 mm in diameter, puberulent with both glandular and eglandular hairs.

Phenology. Flowering occurs from September to November, and fruiting from November to January of the next year.

Etymology. The specific epithet ‘*ochroleuca*’ is derived from its pale yellow corolla. The original epithet ‘*ochro-leuca*’ derived from the Greek, ‘ώχϱα,’ namely ‘*ochra-*,’ means ochre, yellowish and ‘λευκά,’ namely ‘*-lefka*’ means white.

Vernacular name. Huáng Huā Hé Chí Bào Chūn Jù Tái (Chinese pronunciation); 黄花河池报春苣苔 (Chinese name).

Distribution and habitat. *Primulina hochiensis* var. *ochroleuca* is hitherto only known from the type locality, Xiling Town, Gongcheng County, Guangxi Zhuang

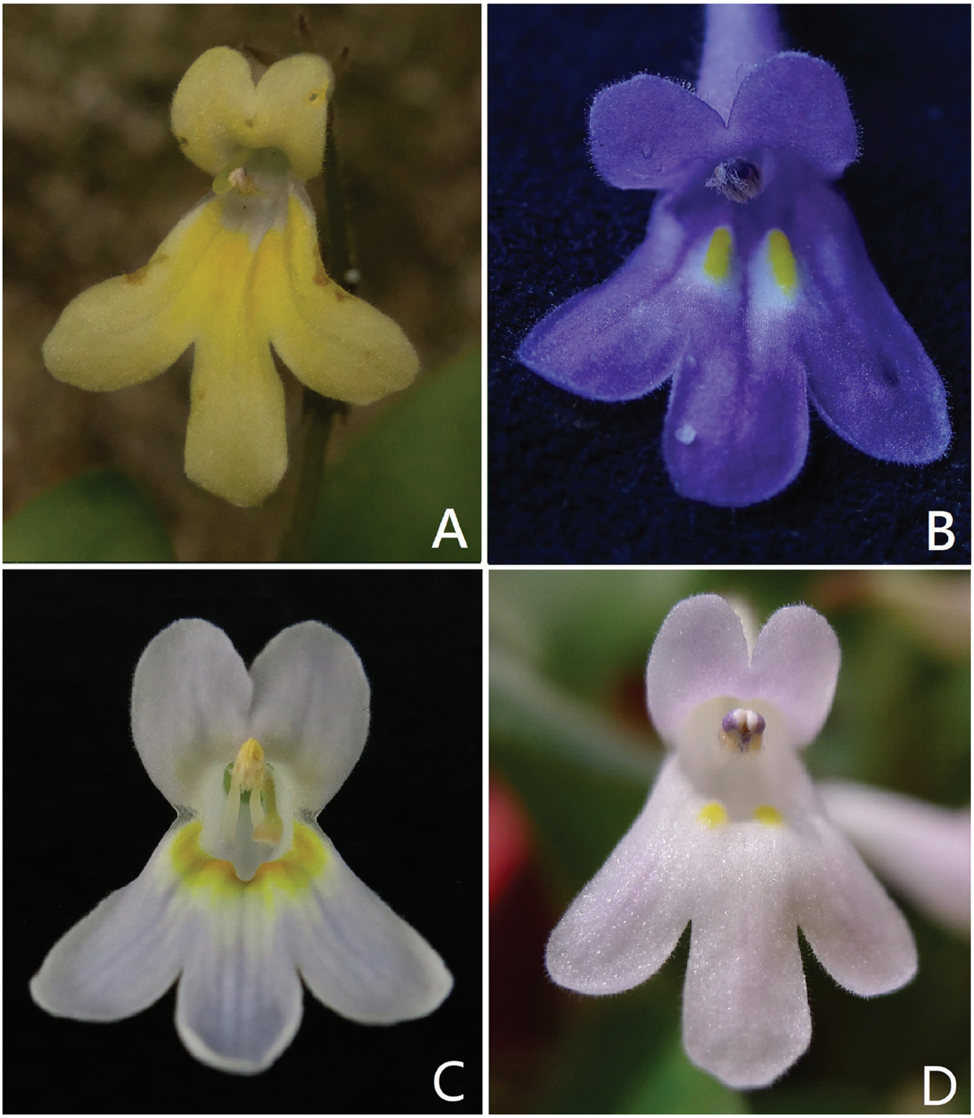

Figure 2. Comparison of frontal view of corolla between *Primulina hochiensis* var. *ochroleuca* and the most closely related taxa **A** *P. hochiensis* var. *ochroleuca* **B** *P. hochiensis* var. *hochiensis* **C** *P. hochiensis* var. *ovata* **D** *P. hochiensis* var. *rosulata* (**A, B, D** Photographed by Fang Wen; **C** Photographed by Li-Hua Yang).

Autonomous Region, South China (Fig. 3), and grows on moist and shaded rocky surfaces on the cliff in subtropical evergreen seasonal rain forest.

Preliminary Conservation status. The type population consists of approx. 3000 mature individuals, all growing on moist and shaded rocky surfaces on the cliff. They are easily disturbed by human activities because the distance from the type locality to the local village is short. Parts of vegetation of the type hill have been cleared by local

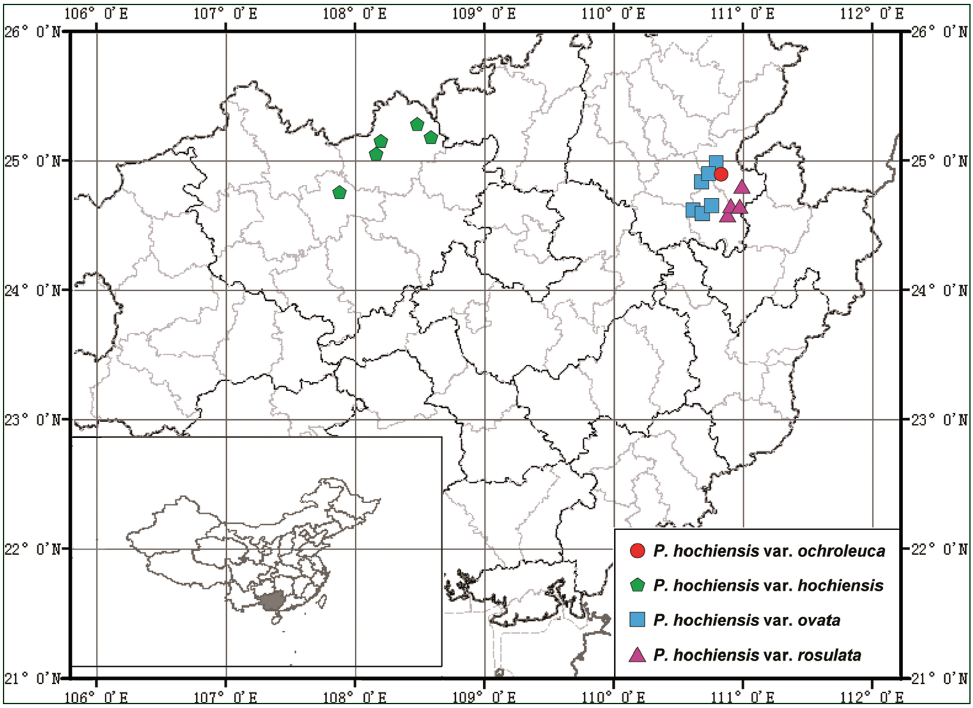

Figure 3. Geographical distribution of the *Primulina hochiensis* var. *ochroleuca* and the most closely related taxa.

people for fruit trees cultivation. Thus, following the IUCN Red List Categories and Criteria (IUCN 2019), it is temporarily assessed as vulnerable [VU C1].

Additional specimens examined. ***Primulina hochiensis*** (C.C. Huang & X.X. Chen) Mich. Möller & A. Weber var. ***hochiensis***, China: Guangxi, Hechi City, 23 October 1991, *C.C. Huang 19670* (Holotype: GXMI!); Huanjiang County, Shuiyuan Town to Xianan Town, limestone hill, 24°49'34.25"N, 108°01'59.01"E, 249 m, 19 Jul. 2013, *451226130719009LY* (GXMG!; IBK!). ***Primulina hochiensis*** (C.C. Huang & X.X. Chen) Mich. Möller & A. Weber var. ***ovata*** L.H. Yang, H.H. Kong & M. Kang, China: Guangxi, Guilin City, Pingle County, Pingle Town, Mawei Village, grows on moist limestone rocks at a lower elevation (150–300 m), 18 June 2016, *L.H. Yang PLMW* (holotype: IBSC!); Pingle County, Ertang Town, Da’e’shan Village, 18 June 2016, *L.H. Yang PLET* (IBSC!); Pingle County, Shazi Town, Bao’an Village, 20 June 2016, *L.H. Yang PLSZ* (IBSC!); Pingle County, Pingle Town, Taiping Village, 6 July 2016, *L.H. Yang and M. Kang PLMW* (IBSC!); Gongcheng County, Xiling Town, Huzimiao Village, 19 June 2016, *L.H. Yang GCXL01* (IBSC!); Gongcheng County, Xiling Town, Panyan Village, 19 June 2016, *L.H. Yang GCXL02* (IBSC!). ***Primulina hochiensis*** (C.C. Huang & X.X. Chen) Mich. Möller & A. Weber var. ***rosulata*** F. Wen & Y.G. Wei, China: Guangxi, Guilin City, Pingle County, Tong’an Town, growing in the entrance of a limestone cave, 24°34’47"N, 110°55'34"E, elevation ca. 149 m, 17 August 2008 (fl.), *B. Gao 08171* (holotype IBK!; isotype BJFC!); Gongcheng County, Lianhua Town, on moist limestone rock faces in ev-

Table 1. Morphological comparisons of *Primulina hochiensis* var. *ochroleuca* and the most closely related taxa.

Characters	***P. hochiensis* var. *ochroleuca***	***P. hochiensis* var. *hochiensis***	***P. hochiensis* var. *ovata***	***P. hochiensis* var. *rosulata***
Stolon	lacking	**conspicuous**	**conspicuous**	lacking
Size of petiole	5–7 × 0.4–0.5 cm	**1–3.5 × ca. 0.3 cm**	**2–4.5 × 0.2–0.4 cm**	3.0–5.5 × 0.2–0.4 cm
Length of pedicel	1.5–2 cm	0.7–2.3 cm	**0.8–1.2 cm**	**≤ 0.7 cm**
Size of calyx	3.5–4 × 1–1.2 mm	4–7 × 0.5–0.8 mm	**4.5–6 × 1–1.5 mm**	**7–7.5 × 1.5–2.3 mm**
Color of corolla	pale yellow	**dark purple**	**pale purple or white**	**white or pale pink**
Throat	1 big patch	**2 small spots**	1 big patch	**2 small spots**
No. of staminodes	3	**2**	3	3
Length of pistil	14–18 mm	15–20 mm	16–18 mm	**9.2–9.7 mm**

Note: The bold words mean the key differences between each variety and the new one.

ergreen broadleaved forest and bushes, located in the subtropical monsoon region, 161 m a.s.l., 11 Jul 2012, *Hui-Ling Liang, Yan-Cai Shi & De-Xin Kong, 120711* (IBK!).

Notes. The morphological comparisons between *P. hochiensis* var. *ochroleuca* and the most closely related taxa (*P. hochiensis* var. *hochiensis*, *P. hochiensis* var. *ovata* and *P. hochiensis* var. *rosulata*) are provided in Table 1.

Key to the varieties of the *Primulina hochiensis* complex

1 Stolon conspicuous **2**
– Stolon lacking **3**
2 With 2 small spots at throat of the corolla ..... **1. *P. hochiensis* var. *hochiensis***
– With 1 big patch at throat of the corolla .... **2. *P. hochiensis* var. *ovata***
3 With 2 small spots at throat of the corolla .... **3. *P. hochiensis* var. *rosulata***
– With 1 big patch at throat of the corolla ...... **4. *P. hochiensis* var. *ochroleuca***

In Li et al. (2019), five new species belonging to the genus *Primulina* were described. The correct collection dates and the type specimens numbers of these are as follows:

Page 79, ***Primulina purpureokylin*** **F. Wen, Yi Huang & W. Chuen Chou**

The correct collection date of the type specimens of *Primulina purpureokylin* is 16 Nov 2017, not 3 Apr 2018.

Page 81, ***Primulina persica*** **F. Wen, Yi Huang & W. Chuen Chou**

The correct collection date and the number of the type specimens of *Primulina persica* is 25 Apr 2017, *Chou Wei Chuen et al. CWC170425-01*.

Page 83 ***Primulina cerina*** **F. Wen, Yi Huang & W. Chuen Chou**

The correct collection date and the number of the type specimens of *Primulina cerina* is 14 Apr 2017, *Chou Wei Chuen et al. CWC170414-01*.

Page 85 ***Primulina niveolanosa*** **F. Wen, S. Li & W. Chuen Chou**

The correct collection date and the number of the type specimens of *Primulina niveolanosa* are 8 Jun 2017, *Chou Wei Chuen et al. CWC170608-01*.

Page 87 ***Primulina leiyyi*** **F. Wen, Z. B. Xin & W. Chuen Chou**

The correct collection date of the type specimens of *Primulina leiyyi* is 8 Dec 2018, not 3 Apr 2018.

Acknowledgments

We thank Michael LoFurno, Adjunct Professor, Temple University, Philadelphia, USA, for his editorial assistance. We also want to thank Dr. Li-Hua Yang for his beautiful photograph of *Primulina hochiensis* var. *ovata*. This study was financially supported by the Foundation of Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain (19-050-6), the Guangxi Natural Science Foundation (2017GXNSFAA198006), the National Natural Science Foundation (31860047), Science Research Foundation of Guangxi Academy of Sciences (no. 2017YJJ23022) and the Key Sci. & Tech. Research & Development Project of Guangxi (Guike AB16380053; Guikeneng 1598025-45), Basal Research Fund of GXIB (Guizhiye20009), 21st Talent project of "Ten-Hundred-Thousand" in Guangxi, Guilin Science and Technology Foundation (20180107-6), and the STS Program of the Chinese Academy of Sciences (Grant No. KFJ-3W-No1).

References

Hance HF (1883) New Chinese Cyrtandreae. Le Journal de Botanique 21: 165–170.

Hao Z, Kuang YW, Kang M (2015) Untangling the influence of phylogeny, soil and climate on leaf element concentrations in a biodiversity hotspot. Functional Ecology 59(2): 165–176. https://doi.org/10.1111/1365-2435.12344

Huang CC, Chen XX (1992) A new medicinal species of *Chirita* (Gesneriaceae) from Guangxi. Botanical Journal of South China 1: 14–16.

IPNI (2020) The International Plant Names Index. http://www.ipni.org [accessed May 2020]

IUCN (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Subcommittee of the IUCN Species Survival Commission. http://cmsdocs.s3.amazonaws.com/RedListGuidelines.pdf

Kang M, Tao J, Wang J, Ren C, Qi Q, Xiang QY, Huang HW (2014) Adaptive and nonadaptive genome size evolution in karst endemic flora of China. The New Phytologist 202(4): 1371–1381. https://doi.org/10.1111/nph.12726

Kong HH, Condamine FL, Harris AJ, Chen JL, Pan B, Möller M, Hoang VS, Kang M (2017) Both temperature fluctuations and East Asian monsoons have driven plant diversification in the karst ecosystems from southern China. Molecular Ecology 26(22): 6414–6429. https://doi.org/10.1111/mec.14367

Li S, Xin ZB, Chou WC, Huang Y, Pan B, Maciejewski S, Wen F (2019) Five new species of the genus *Primulina* (Gesneriaceae) from limestone areas of Guangxi Zhuangzu autonomous region, China. PhytoKeys 127: 77–91. https://doi.org/10.3897/phytokeys.127.35445

Liang HL, Kong DX, Shi YC, Zhao B, Wen F (2013) *Primulina tsoongii* sp. nov. (Gesneriaceae) from a limestone area in north Guangxi, China. Nordic Journal of Botany 32(1): 75–79. https://doi.org/10.1111/j.1756-1051.2013.00306.x

Möller M (2019) Species Discovery in Time: An Example from Gesneriaceae in China. Guangxi Sciences 26(1): 1–16.

Möller M, Wei YG, Wen F, Clark JL, Weber A (2016) You win some you lose some: Updated generic delineations and classification of Gesneriaceae-implications for the family in China. Guihaia 36: 44–60.

Ning ZL, Pan B, Wen F, Kang M, Zhuang XY (2016) *Primulina yingdeensis*, a new species from Guangdong, China, and *P. rosulata*, a new combination (Gesneriaceae), based on morphological and molecular evidence. Willdenowia 46(3): 399–409. https://doi.org/10.3372/wi.46.46308

Pan B, Xu MZ, Tang WX, Yang LH (2020) *Primulina zixingensis* (Gesneriaceae), a new species from Hunan, China. Annales Botanici Fennici 57(1–3): 55–59. https://doi.org/10.5735/085.057.0107

Tropicos (2020) Tropicos.org. Missouri Botanical Garden. http://www.tropicos.org [accessed May 2020]

Vu PX (2018) Gesneriaceae. In: Tran TH (Ed.) Flora of Vietnam. (Vol. 18). Technology & Science Publishing House, Hanoi.

Wang YZ, Mao RB, Liu Y, Li JM, Dong Y, Li ZY, Smith JF (2011) Phylogenetic reconstruction of *Chirita* and allies (Gesneriaceae) with taxonomic treatments. Journal of Systematics and Evolution 49(1): 50–64. https://doi.org/10.1111/j.1759-6831.2010.00113.x

Weber A, Middleton DJ, Forrest A, Kiew R, Lim CL, Rafidah AR, Sontag S, Triboun P, Wei YG, Yao TL, Möller M (2011) Molecular systematics and remodeling of *Chirita* and associated genera (Gesneriaceae). Taxon 60(3): 767–790. https://doi.org/10.1002/tax.603012

Wen F, Qin GL, Wei YG, Liang GY, Gao B (2012) *Primulina hochiensis* var. *rosulata* (Gesneriaceae)–A new variety at an entrance of a limestone cave from Guangxi, China. Phytotaxa 54: 37–42. https://doi.org/10.11646/phytotaxa.54.1.4

Wen F, Li S, Xin ZB, Fu LF, Cai L, Qin JQ, Pan B, Hong X, Pan FZ, Wei YG (2019) The Updated Plant List of Gesneriaceae in China against the Background of Newly Chinese Naming Rules. Guangxi Sciences 26(1): 37–63.

Wen F, Wei YG, Fu LF, Xin ZB, Li S, Huang ZJ, Meng DC (2020) The Checklist of Gesneriaceae in China. http://gccc.gxib.cn/about–46.aspx. [accessed 15 May 2020]

Yang LH (2018) Species delimitation of *Primulina hochiensis* complex, with some field investigations and taxonomic studies on Gesneriaceae of South China. PhD Thesis, University of Chinese Academy of Sciences, China.

Yang LH, Kong HH, Huang JP, Kang M (2019) Different species or genetically divergent populations? Integrative species delimitation of the *Primulina hochiensis* complex from isolated karst habitats. Molecular Phylogenetics and Evolution 132: 219–231. https://doi.org/10.1016/j.ympev.2018.12.011

PhytoKeys 152: 121–136 (2020)
doi: 10.3897/phytokeys.152.50611
http://phytokeys.pensoft.net

RESEARCH ARTICLE

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Splitting the *Pisonia* birdcatcher trees: re-establishment of *Ceodes* and *Rockia* (Nyctaginaceae, Pisonieae)

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Academic editor: Alexander Sukhorukov | Received 29 January 2020 | Accepted 8 April 2020 | Published 7 July 2020

Citation: Rossetto EFS, Caraballo-Ortiz MA (2020) Splitting the *Pisonia* birdcatcher trees: re-establishment of *Ceodes* and *Rockia* (Nyctaginaceae, Pisonieae). PhytoKeys 152: 121–136. https://doi.org/10.3897/phytokeys.152.50611

Abstract

Several genera of Nyctaginaceae, currently merged under *Pisonia*, have been described for the Indo-Pacific region. Results from a recent molecular phylogenetic study of tribe Pisonieae showed that *Pisonia* is non-monophyletic and comprises three well-supported lineages: one including typical *Pisonia* and allies (*Pisonia* s.str.), a clade of species which corresponds to the original description of *Ceodes* and a third lineage whose single representative was formerly treated under the monotypic genus *Rockia*. Thus, as part of an effort to achieve a natural classification for tribe Pisonieae, this work proposes to re-establish *Ceodes* and *Rockia* to accommodate taxa with inconspicuous glands on anthocarps, recognising 21 species (20 for the former and one for the latter), of which 16 are new combinations: *Ceodes amplifolia* **comb. nov.**, *Ceodes artensis* **comb. nov.**, *Ceodes austro-orientalis* **comb. nov.**, *Ceodes brownii* **comb. nov.**, *Ceodes cauliflora* **comb. nov.**, *Ceodes coronata* **comb. nov.**, *Ceodes diandra* **comb. nov.**, *Ceodes gigantocarpa* **comb. nov.**, *Ceodes gracilescens* **comb. nov.**, *Ceodes lanceolata* **comb. nov.**, *Ceodes merytifolia* **comb. nov.**, *Ceodes muelleriana* **comb. nov.**, *Ceodes rapaensis* **comb. nov.**, *Ceodes sechellarum* **comb. nov.**, *Ceodes taitensis* **comb. nov.** and *Ceodes wagneriana* **comb. nov.** A general distribution of each species recognised in this work is also included, along with line drawings and colour pictures of representative species of *Ceodes*, *Pisonia* and *Rockia* and an updated dichotomous key based on reproductive characters for the nine genera (*Ceodes*, *Cephalotomandra*, *Grajalesia*, *Guapira*, *Neea*, *Neeopsis*, *Pisonia*, *Pisoniella* and *Rockia*) comprising the tribe Pisonieae.

Résumé

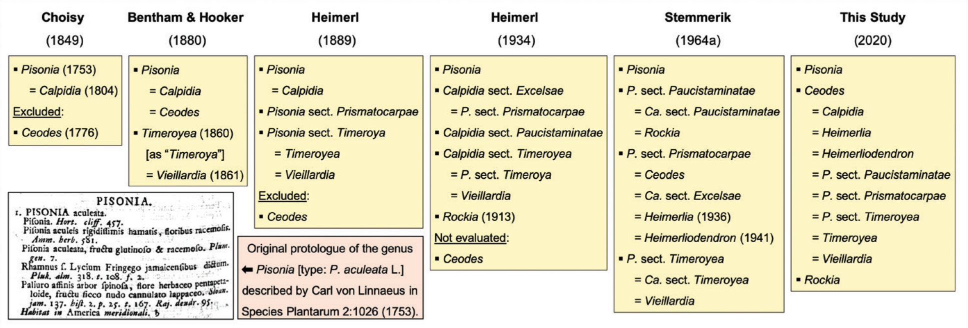
Plusieurs genres de Nyctaginaceae actuellement fusionnés sous *Pisonia* ont été décrits pour la région Indo-Pacifique. Les résultats d'une récente étude phylogénétique moléculaire de la tribu Pisonieae ont montré que *Pisonia* est non monophylétique et comprend trois lignées bien supportées: une comprenant *Pisonia* typique et ses alliés (*Pisonia* s.str.), un clade d'espèces qui correspond à la description originale de *Ceodes* et une troisième lignée dont l'unique représentant était auparavant traité sous le genre monotypique *Rockia*. Ainsi, dans le cadre d'un effort pour parvenir à une classification naturelle de la tribu Pisonieae, ce travail proposons de rétablir les *Ceodes* et *Rockia* pour accueillir des taxons avec des glandes discrètes sur les anthocarpes, reconnaissant 21 espèces (20 pour les premières et une pour les dernières), dont 16 sont de nouvelles combinaisons: *Ceodes amplifolia* **comb. nov.**, *Ceodes artensis* **comb. nov.**, *Ceodes austro-orientalis* **comb. nov.**, *Ceodes brownii* **comb. nov.**, *Ceodes cauliflora* **comb. nov.**, *Ceodes coronata* **comb. nov.**, *Ceodes diandra* **comb. nov.**, *Ceodes gigantocarpa* **comb. nov.**, *Ceodes gracilescens* **comb. nov.**, *Ceodes lanceolata* **comb. nov.**, *Ceodes merytifolia* **comb. nov.**, *Ceodes muelleriana* **comb. nov.**, *Ceodes rapaensis* **comb. nov.**, *Ceodes sechellarum* **comb. nov.**, *Ceodes taitensis* **comb. nov.** et *Ceodes wagneriana* **comb. nov.** Une distribution générale de chaque espèce reconnue dans ce travail est également incluse, ainsi que des dessins au trait et des images en couleur des espèces représentatives de *Ceodes*, *Pisonia* et *Rockia*, et préparé une clé dichotomique mise à jour basée sur les caractères reproductifs des neuf genres (*Ceodes*, *Cephalotomandra*, *Grajalesia*, *Guapira*, *Neea*, *Neeopsis*, *Pisonia*, *Pisoniella* et *Rockia*) comprenant la tribu Pisonieae.

Keywords
Calpidia, Caryophyllales, flora of Hawaii, flora of the Indo-Pacific, flora of oceanic islands, *Heimerliodendron*, island endemics, *Timeroyea*

Introduction

The tribe Pisonieae Meisn. in Nyctaginaceae (Caryophyllales) contains the most diverse woody assemblage of the family, represented by over 200 species distributed mainly in the tropical and subtropical regions of the New World (Douglas and Spellenberg 2010). Although members of Pisonieae are present – and often common – in all types of Neotropical habitats and are important components for many ecosystems, taxonomic delimitations at the generic and species levels are still obscure and in urgent need of updated treatments. The tribe currently comprises seven accepted genera (*Cephalotomandra* H.Karst & Triana, *Grajalesia* Miranda, *Guapira* Aubl., *Neea* Ruiz & Pav., *Neeopsis* Lundell, *Pisonia* L. and *Pisoniella* (Heimerl) Standl.), all of them restricted to the New World except *Pisonia*, which has a pantropical distribution (Douglas and Spellenberg 2010). However, other genera have been erected in the last three centuries to include some of the Indo-Pacific taxa with dried anthocarps and inconspicuous glands along anthocarp ribs, which have been either recognised as accepted or treated as synonyms of *Pisonia* by different authors, resulting in a convoluted taxonomic history that we aim to clarify below and that is also summarised in Figure 1.

Ceodes J.R. Forst. & G.Forst., which was described by Forster and Forster (1776), is the oldest of the Indo-Pacific genera with its type species *Ce. umbellifera* J.R.Forst. & G.Forst. collected in Tanna Island at Vanuatu, characterised by the absence of stalked glands along the ribs of anthocarps (Seemann 1863). Later, Du Petit-Thouars (1804) established the genus *Calpidia* Thouars, whose detailed description is based on material collected in Mauritius and which, just as *Ceodes*, differed from *Pisonia*, mainly by the absence of glandular emergences on the surface of its anthocarps (Du Petit-Thouars 1806; see Figs 2, 3). The protologues of *Ceodes* and *Calpidia* describe essentially the same diagnostic characters and it is possible that Du Petit-Thouars was unaware that



PISONIA.
1. PISONIA aculeata.
Piſonia. *Hort. cliff.* 457.
Piſonia aculeis rigidiſſimis hamatis, floribus racemoſis. *Amm. herb.* 581.
Piſonia aculeata, fructu glutinoſo & racemoſo. *Plum. gen.* 7.
Rhamnus ſ. Lycium Fringego jamaicenſibus dictum. *Pluk. alm.* 318. *t.* 108. *f.* 2.
Paliuro affinis arbor ſpinoſa, flore herbaceo pentapetaloide, fructu ſicco nudo cannulato lappaceo. *Sloan. jam.* 137. *hiſt.* 2. *p.* 25. *t.* 167. *Raj. dendr.* 95.
Habitat in America *meridionali.* ♄

Figure 1. Diagram depicting the history of classification for *Calpidia*, *Ceodes*, *Heimerliodendron*, *Pisonia* and *Rockia*. Major taxonomic treatments are shown within boxes. Authors are shown in bold and publication years of treatments and genera within parentheses.

Ceodes had been described 28 years earlier, as he did not mention this genus in either of his two publications on *Calpidia*.

In a global treatment of Nyctaginaceae, prepared by Choisy (1849), he merged *Calpidia* under *Pisonia* and, as with Du Petit-Thouars, he did not include *Ceodes* in this treatment. Over 30 years later, Bentham and Hooker (1880) maintained both *Calpidia* and *Ceodes* as synonyms of *Pisonia*. However, they recognised the monotypic genus *Timeroyea* Montrouz. (using the orthographic variant "*Timeroya*") from New Caledonia, which besides *Ceodes* and *Calpidia*, represents a third genus with inconspicuous glands on its anthocarps, but was characterised by having many (25–30) stamens (Montrouzier 1860; Beauvisage 1901).

Nine years after Bentham and Hooker's publication, Heimerl (1889) presented his first tribal treatment for Nyctaginaceae, in which he split *Pisonia* into six sections, resulting in an expanded delimitation of this genus. *Timeroyea* was reduced to a section of *Pisonia* (as *P*. sect. *Timeroya*), while *P.* sect. *Prismatocarpae* was established to accommodate taxa with up to 15 stamens, resulting in two sections of *Pisonia* with inconspicuously-glanded taxa. In this treatment, *Calpidia* was listed as a synonym of *Pisonia*, while *Ceodes* was not mentioned at all.

Subsequent work by Heimerl (1913a), based on the examination of additional material, led him to propose the split of *Pisonia* sensu lato with the reinstatement of *Calpidia* to embrace all taxa placed under *P.* sect. *Prismatocarpae* and *P.* sect. *Timeroya*. Here, *Calpidia* differed from other *Pisonia* sections by the absence of bracteoles, having a reduced perisperm that forms gelatinous traces and starch accumulation in the embryo and by its geographic distribution. In the following publication which included palynological analysis, Heimerl (1913b) proposed new combinations to *Calpidia*, including some of the newly described species by Warburg (1891) and Bargagli-Petrucci (1901) and described the monotypic genus *Rockia* Heimerl to accommodate the Hawaiian endemic *P. sandwicensis* Hillebr. Although the anthocarps of *Rockia* have inconspicuous glands located along the ribs, Heimerl (1913b) distinguished it from *Calpidia* by the presence of bracteoles and the number of pores in pollen grains, where *Rockia* has sessile flowers with one bract and two bracteoles at its base and tricolpate pollen, while *Calpidia* has pedicellate flowers lacking any bracts or bracteoles at the upper portion of the pedicels and pollen with four or more colpi, resulting in many apertures.

In his last comprehensive synthesis of Nyctaginaceae, Heimerl (1934) maintained *Rockia* as an accepted genus and additionally recognised three sections in *Calpidia*, based on the presence of a rostrum – a beaked or filamentous extension at the apex of the anthocarps – and the number of stamens: *Ca.* sect. *Excelsae* (= *P.* sect. *Prismatocarpae*), *Ca.* sect. *Paucistaminatae* and *Ca.* sect. *Timeroyea*. *Calpidia* sect. *Timeroyea*, represented by the New Caledonian endemic *Ca. artensis* (Montrouz.) Heimerl, is characterised by flowers with a high number of stamens (≥ 30), while the Indo-Pacific widespread *Ca.* sect. *Excelsae*, which includes *Ca. excelsa* (Blume) Heimerl and *Ca. brunoniana* (Endl.) Heimerl, has flowers with 6–30 stamens. On the other hand, species with less than five stamens and a rostrum were placed into *Ca.* sect. *Paucistaminatae*, most of whose representatives occur in Papua New Guinea (e.g. *Ca. longirostris* (Teijsm. & Binn.) Heimerl).

Unlike with his former treatment, Heimerl (1934) mentioned *Ceodes*, but did not evaluate its status under the argument that he lacked enough information about this genus to reach a taxonomic decision, even when Skottsberg (1926), years before, had acknowledged the priority of *Ceodes* over *Calpidia*. Skottsberg re-established *Ceodes* under the argument that there were extant original specimens and that the scant description of the genus was similar to other names published during the late 18th century. However, Skottsberg's treatment was restricted to the plants from Hawaiʻi and included only two species in *Ceodes* (*Ce. brunoniana* (Endl.) Skottsb. and *Ce. forsteriana* (Endl. ex Walp.) Skottsb.) and listed a third one (*Ce. excelsa* (Blume) Skottsb.) as a questionable species. As Heimerl (1934) still did not accept *Ceodes* and retained *Calpidia* in his new treatment of Nyctaginaceae, Skottsberg (1936) published a work focused on the nyctaginaceous trees from Hawaiʻi where he reinstated his views on the priority of *Ceodes*, this time recognising only one species (*Ce. umbellifera*, including *Ce. excelsa* and *Ce. forsteriana* as synonyms). In this same work, he also described the genus *Heimerlia* Skottsb. to accommodate *Ce. brunoniana*, a species characterised by having hermaphroditic flowers. Following Skottsberg's views, Heimerl (1937) finally accepted the priority of *Ceodes* over *Calpidia* and described a new form for *Ce. umbellifera* (*Ce. umbellifera* f. *amplifolia* Heimerl), but did not effectuate any transfers from the sections of *Calpidia* he previously published. Two years later, in their first paper on a series of publications on the plants from Papua New Guinea, Merrill and Perry (1939) proposed two new combinations for species of *Ceodes*. Finally, Skottsberg (1941) corrected the name *Heimerlia* to *Heimerliodendron* Skottsb. after noticing that the former had been already described for a fungus.

In a new and drastically different treatment for the group, Stemmerik (1964a) proposed a broad definition for *Pisonia* which re-incorporated all taxa with inconspicuous glands along anthocarps. In his revision, which was restricted to the Indo-Pacific taxa, he merged *Calpidia*, *Ceodes*, *Heimerliodendron* and *Rockia* within *Pisonia*. The three sections of *Calpidia*, recognised by Heimerl in 1934, were transferred to *Pisonia*, where *P.* sect. *Prismatocarpae* sensu Heimerl (1889) (same as *Ca.* sect. *Excelsae* sensu Heimerl 1934) was restored. *Rockia* was merged into *P.* sect. *Paucistaminatae* (sensu Heimerl 1934) along with the taxa with pedicellate flowers and having an anthocarp rostrum. Therefore, the delimitation of the three sections of *Pisonia*, proposed by Stemmerik (1964a), was based on characters used by Heimerl (1934) to define his sectional ranks, such as type of glands on anthocarps, presence of a rostrum and number of stamens. However, he did not consider the absence of bracts and bracteoles at the upper portion of the pedicels, presence of starch in the embryo and number of apertures in pollen grains, as he argued that at least the pollen structure was not a constant character and, therefore, had no utility separating genera (Stemmerik 1964b).

A recent phylogenetic study of tribe Pisonieae, based on molecular data (Rossetto et al. 2019), indicated that *Pisonia*, as delimitated by Stemmerik (1964a, b), is non-monophyletic. The current definition of *Pisonia* places taxa with inconspicuous glands along anthocarp ribs (Fig. 3A–C, F) into two distinct, well-supported lineages (i.e. clades A and C sensu Rossetto et al. 2019; Fig. 4), while typical *Pisonia* and its allies with glandular emergences (Fig. 3D–E) are restricted to clade B (*Pisonia* s.str.; Fig. 4). In clade A, formed by taxa carrying pedicellate flowers without bracteoles, members of the *P.* sect. *Prismatocarpae* and *P.* sect. *Timeroyea* (sensu Stemmerik 1964a) are included in the clade Ceodes, although these sections were not clustered in natural groups. Concurrently, *P. sandwicensis* from the *P.* sect. *Paucistaminatae* is placed in clade C as sister to the Neotropical genera *Guapira* and *Neea* (Rossetto et al. 2019; Fig. 4). Therefore, in order to simplify the classification of the tribe by designating monophyletic genera for the two independent lineages with inconspicuous glands within the tribe, it is necessary to resurrect *Ceodes* and *Rockia*. The objective of this work is to re-establish these two genera and to provide new combinations where necessary. To facilitate recognition in herbaria and in the field, we also provide colour pictures and line drawings of representative species of *Ceodes*, *Pisonia* and *Rockia* and a dichotomous key for the nine genera comprising the tribe Pisonieae.

Materials and methods

For the taxonomic treatment, we compiled accepted names following Stemmerik's revision (1964a), which is the most recent comprehensive treatment for Pisonieae in the Pacific region. We also consulted other more recent regional treatments and species descriptions and provided new generic combinations of the taxa that, according to our understanding, are currently considered as accepted (Friedmann 1986; Fosberg 1987; Philcox and Coode 1994; Florence 2004; Whistler 2004). Additional information on geographic distributions was obtained from Heimerl (1913b) and Stemmerik (1964b). Generic descriptions were based on Heimerl (1913b; 1934), while Skottsberg (1936) was used specifically for the description of pollen structure of *Ceodes*.

Results and conclusions

Here we re-established the genera *Ceodes* and *Rockia*, recognising 20 species for the former and one for the latter. Sixteen out of the 20 species, recognised for *Ceodes*, represent new combinations (see Taxonomic treatment section). The re-establishment of *Ceodes* and *Rockia* provides an important step to refine our knowledge of the taxonomy and evolution of Pisonieae from the Indo-Pacific region. This work also has considerable implications for estimates of regional biodiversity, as many species of *Ceodes* are island endemics, while *Rockia* would be a genus restricted to the Hawaiian Archipelago (Wagner et al. 2005).

Some species of Pisonieae have been reported as dominant components of the vegetation from remote islands, in part because their sticky anthocarps can travel long distances attached to the feathers of seabirds (St. John 1951; Airy-Shaw 1952). Therefore, future studies on the taxonomy, ecology and biogeography of Pisonieae will help us understand how interactions with pollinators, seed dispersers (Walker et al. 1991; Murphy and Legge 2003; Burger 2005) and mycorrhiza (Hayward and Hynson 2014) have contributed to promote endemism in trees with a high dispersal capability.

Taxonomic treatment

Ceodes **J.R.Forst. & G.Forst., Char. Gen. Pl., ed. 2: 141. 1776.**

≡ *Pisonia* sect. *Prismatocarpae* Heimerl, Nat. Pflanzenfam. 3(1b): 29. 1889. Type (designated by Stemmerik in Blumea 12: 277. 1964): *Pisonia umbellifera* (J.R.Forst. & G.Forst.) Seem. (≡ *Ceodes umbellifer*a J.R.Forst. & G.Forst.), **syn. nov.**

= *Calpidia* Thouars, Hist. Vég. Îsles Austral. Afriq. 37, pl. 10. 1804. Type: *Calpidia oblonga* J.St.-Hil., **syn. nov.**

= *Heimerlia* Skottsb., Svensk Bot. Tidskr. 30: 738. 1936 (non Höhn. 1903). Type: *Heimerlia brunoniana* (Endl.) Skottsb., **syn. nov.**

= *Heimerliodendron* Skottsb., Svensk Bot. Tidskr. 35: 364. 1941. Type: *Heimerliodendron brunonianum* (Endl.) Skottsb., **syn. nov.**

= *Pisonia* sect. *Paucistaminatae* (Heimerl) Stemm., Blumea 12: 277. 1964 ≡ *Calpidia* sect. *Paucistaminatae* Heimerl, Nat. Pflanzenfam. 16c: 125. 1934. Type (designated by Stemmerik in Blumea 12: 277. 1964): *Pisonia longirostris* Teijsm. & Binn. (≡ *Calpidia longirostris* (Teijsm. & Binn.) Heimerl), **syn. nov.**

= *Pisonia* sect. *Timeroyea* (Montrouz.) Heimerl, Nat. Pflanzenfam. 3(1b): 29. 1889, '*Timeroya*' ≡ *Timeroyea* Montrouz., Mém. Acad. Roy. Sci. Lyon, Sect. Sci. 10: 247. 1860. Type (designated by Stemmerik in Blumea 12: 277. 1964): *Pisonia artensis* (Montrouz.) Barg.-Petr. (≡ *Timeroyea artensis* Montrouz.), **syn. nov.**

= *Vieillardia* Brong. & Gris, Bull. Soc. Bot. France 8: 375. 1861 (non Montrouz. 1860). Type: *Vieillardia austrocaledonica* Brong. & Gris., **syn. nov.**

Type. *C. umbellifera* J.R.Forst. & G.Forst.

Description. *Habit and phyllotaxy.* Dioecious or hermaphroditic trees or shrubs, leaves (sub)opposite or (sub)verticillate clustered at apex of branches.

Inflorescence. Axillary, terminal or occasionally cauliflorous, arranged in compound cymes.

Flowers. Unisexual (with vestiges of another sex) or rarely hermaphrodite, pedicellate, bracteoles absent at the upper portion of the pedicels, perianth campanulate

(Fig. 2A, D) to funnel-shaped, stamens 2 to many (> 30), long or shortly exserted (Fig. 2D) and stigma penicillate or less frequently fimbriate, exserted (Fig. 2A).

Anthocarp. Leathery or woody (but never fleshy), ellipsoid, prismatic or fusiform, sometimes with a rostrum at apex (Fig. 3B) and 4–5 longitudinal ribs with inconspicuous sticky glands (Figs 2B, C, 3A–C).

Pollen. Six and 12 colpi geometrically arranged.

Perisperm. Often scarce, gelatinous or mealy.

1. ***Ceodes amplifolia*** (Heimerl) E.F.S.Rossetto & Caraballo, comb. nov.

urn:lsid:ipni.org:names:77210103-1

≡ *Ceodes umbellifera* f. *amplifolia* Heimerl, Occas. Pap. Bernice Pauahi Bishop Mus. 13: 38. 1937. (Basionym).

Distribution. French Polynesia (Austral Islands) (Florence 2004).

2. ***Ceodes artensis*** (Montrouz.) E.F.S.Rossetto & Caraballo, comb. nov.

urn:lsid:ipni.org:names:77210104-1

≡ *Timeroyea artensis* Montrouz., Mém. Acad. Roy. Sci. Lyon, Sect. Sci. 10: 247. 1860. (Basionym).

Distribution. New Caledonia (Stemmerik 1964a).

3. ***Ceodes austro-orientalis*** (J.Florence) E.F.S.Rossetto & Caraballo, comb. nov.

urn:lsid:ipni.org:names:77210105-1

≡ *Pisonia austro-orientalis* J. Florence, Fl. Polynésie Franç. 2: 307. 2004. (Basionym).

Distribution. French Polynesia (Gambier Islands) (Florence 2004).

4. ***Ceodes brownii*** (J.Florence) E.F.S.Rossetto & Caraballo, comb. nov.

urn:lsid:ipni.org:names:77210106-1

≡ *Pisonia brownii* J.Florence, Fl. Polynésie Franç. 2: 308. 2004. (Basionym).

Distribution. French Polynesia: Nuku Hiva (Florence 2004).

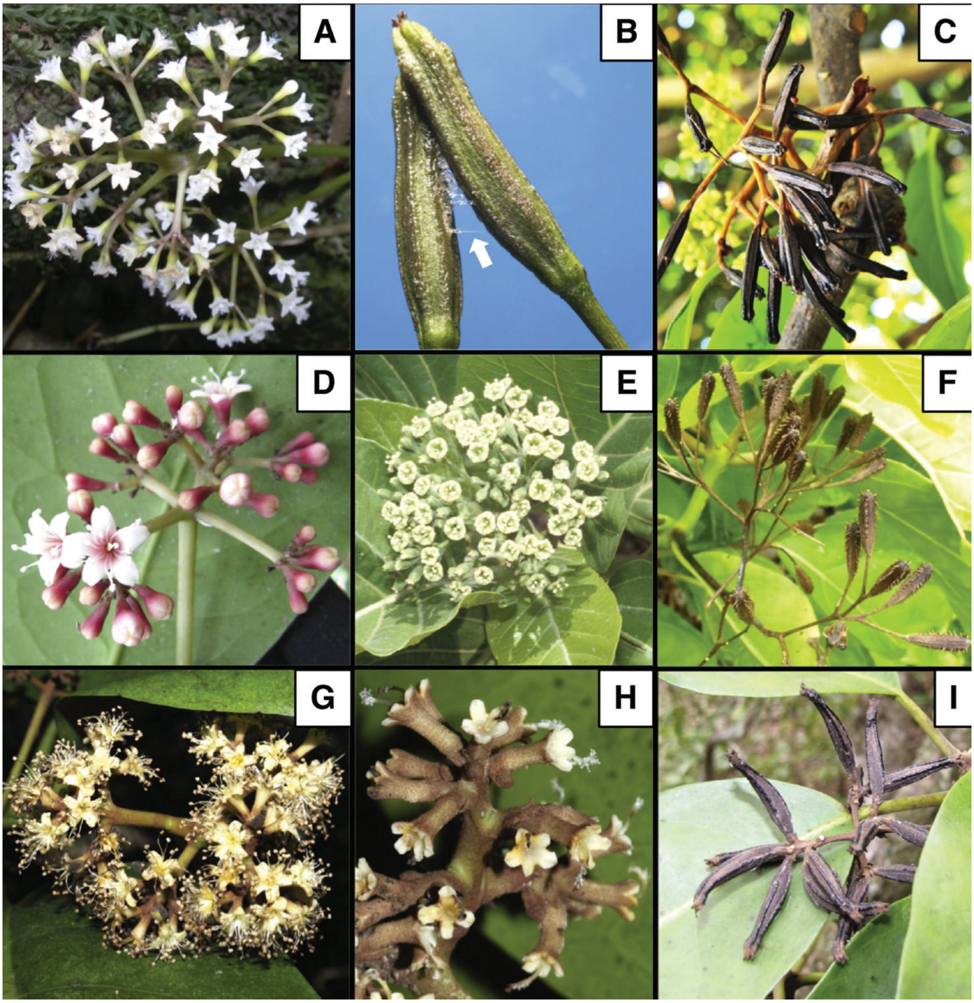


Figure 2. Field images for representative species of *Ceodes*, *Pisonia* and *Rockia* (Nyctaginaceae) from the Pacific Islands **A** *Ceodes taitensis*. Branch with pistillate flowers **B** *Ceodes brunoniana*. Ripe anthocarps (fruits) exuding sticky secretions (arrow) **C, D** *Ceodes umbellifera*. Branch with ripe anthocarps (**C**) and staminate flowers at anthesis (**D**) **E, F** *Pisonia grandis* R.Br. Staminate flowers at anthesis (**E**) and ripe anthocarps (**F**) **G–I** *Rockia sandwicensis*. Staminate (**G**) and pistillate (**H**) flowers at anthesis and ripe anthocarps (**I**) Photo credits: **A, F** by J.-Y. Meyer **B** by L. Jensen **C** by C.-I Peng **D, E, I** by F. Starr and K. Starr **G, H** by K. Magnacca.

5. *Ceodes brunoniana* (Endl.) Skottsb., Acta Horti Gothob. 2: 231. 1926.

Figs 2B, 3A

≡ *Pisonia brunoniana* Endl., Prodr. Fl. Norf. 43. 1833. (Basionym).

Distribution. Hawai‘i (Hawai‘i, Lana‘i, Maui, Moloka‘i, O‘ahu), Lord Howe and Norfolk Islands and New Zealand (Northern Island) (Heimerl 1913b; Wagner et al. 2005).

Note. *Pisonia brunoniana* Endl., which was considered by Stemmerik (1964a) a synonym of *P. umbellifera*, is treated here as an accepted name (as *Ce. brunoniana*), following Sykes (1987), who clarified the key characters to separate both species.

6. *Ceodes cauliflora* (Scheff.) E.F.S.Rossetto & Caraballo, comb. nov.

urn:lsid:ipni.org:names:77210107-1

≡ *Pisonia cauliflora* Scheff., Natuurk. Tijdschr. Ned.-Indië 32: 417. 1872. (Basionym).

Distribution. Mariana Islands, Solomon Islands and Lesser Sunda Islands, Moluccas and western Papua New Guinea (Stemmerik 1964b).

7. *Ceodes corniculata* (Barg.-Petr.) Merr. & L.M.Perry, J. Arnold Arbor. 20: 327. 1939.

≡ *Pisonia corniculata* Barg.-Petr., Nuov. Giorn. Bot. Ital. ser. 2, 8: 615. 1901. (Basionym).

Distribution. Bacan Islands (Moluccas) and western Papua New Guinea (Heimerl 1913b; Stemmerik 1964b).

8. *Ceodes coronata* (Heimerl) E.F.S.Rossetto & Caraballo, comb. nov.

urn:lsid:ipni.org:names:77210108-1

≡ *Ceodes umbellifera* var. *coronata* Heimerl, Occas. Pap. Bernice Pauahi Bishop Mus. 13: 41. 1937. (Basionym).

Distribution. Rapa Iti (French Polynesia) (Florence 2004).

9. *Ceodes diandra* (Pulle) E.F.S.Rossetto & Caraballo, comb. nov.

urn:lsid:ipni.org:names:77210110-1

≡ *Pisonia diandra* Pulle, Nova Guinea 8: 629. 1912. (Basionym).

Distribution. Papua New Guinea (Stemmerik 1964b).

10. *Ceodes gigantocarpa* (Heimerl) E.F.S.Rossetto & Caraballo, comb. nov.

urn:lsid:ipni.org:names:77210111-1

≡ *Calpidia gigantocarpa* Heimerl, Oesterr. Bot. Z. 63: 284. 1913. (Basionym).

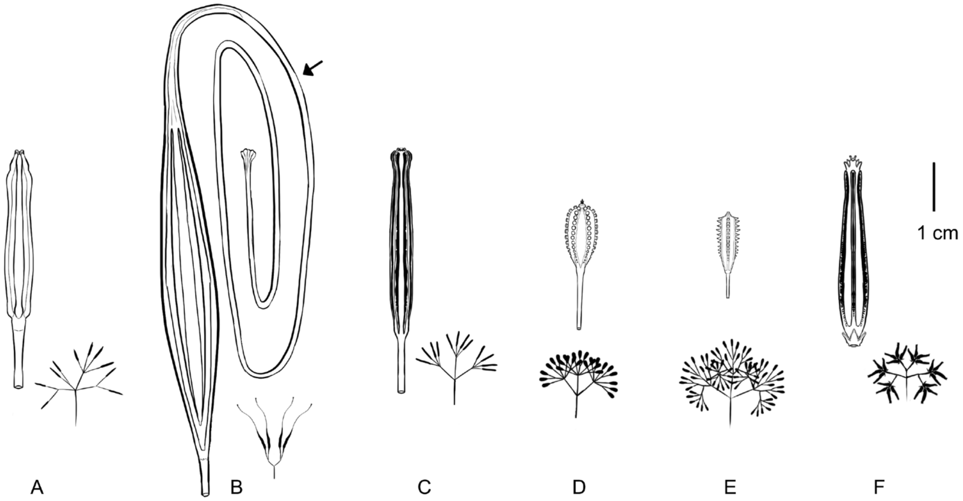


Figure 3. Comparison of size and morphology of ripe fruits (anthocarps) amongst members of *Ceodes*, *Pisonia* and *Rockia* (Nyctaginaceae). The outline of infructescences are shown below each anthocarp **A** *Ceodes brunoniana* (based on *St. John 11272* (US-01258187)) **B** *Ceodes longirostris* (based on *Brass 2972* (HUH-00046918)). Note the extremely long rostrum at the tip of the anthocarp (indicated with an arrow) **C** *Ceodes umbellifera* (based on *Foxworthy 593* (US-03661041)) **D** *Pisonia aculeata* L. (based on *Caraballo 3464* (IJ)) **E** *Pisonia grandis* (based on *Fosberg 24357* (US-00959523)) **F** *Rockia sandwicensis* (based on *Lorence 6305* (US-00452890)). Illustration credit: Ramos Sepúlveda.

Distribution. New Caledonia (Stemmerik 1964a).

11. *Ceodes gracilescens* (Heimerl) E.F.S.Rossetto & Caraballo, comb. nov.
urn:lsid:ipni.org:names:77210112-1

≡ *Calpidia gracilescens* Heimerl, Oesterr. Bot. Z. 63: 285. 1913. (Basionym).

Distribution. Tahiti (French Polynesia) (Florence 2004).

12. *Ceodes lanceolata* (Poir.) E.F.S.Rossetto & Caraballo, comb. nov.
urn:lsid:ipni.org:names:77210113-1

≡ *Calpidia lanceolata* Poir., Encycl. Suppl. 2: 38. 1811. (Basionym).

Distribution. Mauritius and Réunion islands (Philcox and Coode 1994).

Note. We disagree with Stemmerik's (1964a) view on *Pisonia lanceolata* (Poir.) Choisy, which he considered a synonym of *P. umbellifera*. According to Friedmann (1986), *P. lanceolata* is a species with affinities to *P. brunoniana*, from which it can be distinguished by the pattern of incisions in the flower.

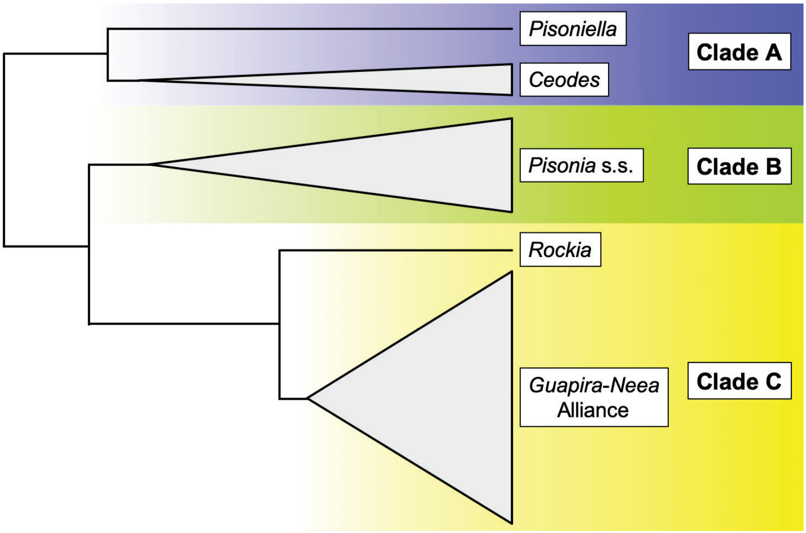


Figure 4. Generic relationships within tribe Pisonieae (Nyctaginaceae) showing the inferred positions of *Ceodes* (Clade A, in blue), *Pisonia* (Clade B, in green) and *Rockia* (Clade C, in yellow) (Rossetto et al. 2019).

13. *Ceodes longirostris* (Teijsm. & Binn.) Merr. & L.M.Perry, J. Arnold Arbor. 20: 328. 1939.

Fig. 3B

≡ *Pisonia longirostris* Teijsm. & Binn., Natuurk. Tijdschr. Ned.-Indië 25: 401. 1863. (Basionym).

Distribution. Solomon Islands, Lesser Sunda Islands, Sulu Archipelago (Philippines), Moluccas and Papua New Guinea (Stemmerik 1964b).

14. *Ceodes merytifolia* (Whistler) E.F.S.Rossetto & Caraballo, comb. nov.

urn:lsid:ipni.org:names:77210114-1

≡ *Pisonia merytifolia* Whistler, Rainforest Trees Samoa: 192. 2004, '*merytafolia*'. (Basionym).

Distribution. Samoa Archipelago (Whistler 2004).

15. *Ceodes muelleriana* (Warb.) E.F.S.Rossetto & Caraballo, comb. nov.

urn:lsid:ipni.org:names:77210115-1

≡ *Pisonia muelleriana* Warb., Bot. Jahrb. Syst. 13: 304. 1891. (Basionym).

Distribution. Solomon Islands and Papua New Guinea (Stemmerik 1964b).

16. *Ceodes rapaensis* (J.Florence) E.F.S.Rossetto & Caraballo, comb. nov.
urn:lsid:ipni.org:names:77210116-1

≡ *Pisonia rapaensis* J.Florence, Fl. Polynésie Franç. 2: 317. 2004. (Basionym).

Distribution. French Polynesia (Rapa Iti) (Florence 2004).

17. *Ceodes sechellarum* (F.Friedmann) E.F.S.Rossetto & Caraballo, comb. nov.
urn:lsid:ipni.org:names:77210117-1

≡ *Pisonia sechellarum* F.Friedmann, Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér. 4, 8: 384. 1986 (publ. 1987). (Basionym).

Distribution. Seychelles (Silhouette Island) (Friedmann 1986).

18. *Ceodes taitensis* (Heimerl) E.F.S.Rossetto & Caraballo, comb. nov.
urn:lsid:ipni.org:names:77210118-1
Fig. 2A

≡ *Calpidia taitensis* Heimerl, Oesterr. Bot. Z. 63: 288. 1913. (Basionym).

Distribution. French Polynesia (Society Islands) (Florence 2004).

19. *Ceodes umbellifera* J.R.Forst & G.Forst., Char. Gen. Pl., ed. 2 142, t. 71. 1776.
Figs 2C, D, 3C

Distribution. Widespread across the Indo-Pacific islands (Pramanick et al. 2015).

20. *Ceodes wagneriana* (Fosberg) E.F.S.Rossetto & Caraballo, comb. nov.
urn:lsid:ipni.org:names:77210119-1

≡ *Pisonia wagneriana* Fosberg, Phytologia 62: 177. 1987. (Basionym).

Distribution. Hawai‘i (Kaua‘i) (Fosberg 1987).

***Rockia* Heimerl, Oesterr. Bot. Z. 63: 289. 1913.**

Type. *R. sandwicensis* (Hillebr.) Heimerl.

Description. ***Habit and phyllotaxy.*** Dioecious trees or shrubs, leaves (sub)opposite or (sub)verticillate clustered at apex of branches.

Inflorescence. Axillary, terminal, arranged in compound cymes.

Flowers. Unisexual (with vestiges of another sex), sessile, with one bract and two bracteoles present at the base, male perianth campanulate, stamens 10–26, exserted (Fig. 2G), female perianth tubular or fusiform (Fig. 2H), stigma fimbriate, exserted.

Anthocarp. Leathery, elongated fusiform, with 5 ribs covered by inconspicuous glands excreting sticky substances (Figs 2I, 3F).

Pollen. Tricolpate, with 3 apertures distant 120° from each other.

Perisperm. Abundant, gelatinous.

1. *Rockia sandwicensis* (Hillebr.) Heimerl, Oesterr. Bot. Z. 63: 290. 1913.
Figs 2G–I, 3F

≡ *Pisonia sandwicensis* Hillebr., Fl. Hawaiian Isl. 369. 1888. (Basionym).

Distribution. Hawai‘i (Hawai‘i, Kaua‘i, Lana‘i, Maui, Moloka‘i, O‘ahu) (Stemmerik 1964a; Wagner et al. 2005).

Key to genera from tribe Pisonieae

The following dichotomous key is compiled to separate the nine currently accepted genera within Pisonieae, based on reproductive features because vegetative (i.e. leaves and twigs) characters do not seem to provide enough resolution to help set apart these genera. Unfortunately, members of Pisonieae tend to have fugacious reproductive seasons and many collections in herbaria lack flowers and/or fruits. Thus, we support the recommendation made by Caraballo-Ortiz and Trejo-Torres (2017) on preparing multiple vouchers from a plant or population across seasons to document the full phenology of species and their range of morphological variation.

1 Staminate flowers with inserted stamens **2**
– Staminate flowers with exserted stamens **4**
2 Stamens about 30 .... ***Cephalotomandra***
– Stamens 5–13 .... **3**
3 Leaves drying blackish; inflorescences in corymbose cymes; flowers usually with urceolate corolla. Widespread across the Neotropics .... ***Neea***
– Leaves greenish when dry; inflorescences in dichasium; flowers with campanulate corolla. Restricted to Guatemala .... ***Neeopsis***
4 Flowers pedicellate, lacking bracts or bracteoles at the upper portion of the pedicels **5**
– Flowers sessile, subtended by one bract and two bracteoles **6**

5 Inflorescence in simple umbel; glandular emergences along anthocarp ribs. Neotropics .... ***Pisoniella***
– Inflorescence in compound cymes; inconspicuous glands along anthocarp ribs. Indo-Pacific .... ***Ceodes***
6 Anthocarps red- or violet coloured, more or less fleshy when ripe .... ***Guapira***
– Anthocarps dry when ripe 7
7 Anthocarps winged, lacking sticky glands .... ***Grajalesia***
– Anthocarps not winged, sticky glands present **8**
8 Anthocarp ribs covered by glandular emergences. Pantropical .... ***Pisonia***
– Anthocarp ribs covered by inconspicuous glands. Endemic to Hawai'i .... ***Rockia***

Acknowledgements

The authors thank Dr. Alexander Sukhorukov (Lomonosov Moscow State University) for translating texts from German and constructive editorial suggestions. We also appreciate the useful comments provided by Dr. Lucas Majure (Florida Museum of Natural History) to improve the quality of this manuscript. The artist Ramos Sepúlveda (Puerto Rico) prepared the elegant line drawings presented in Figure 3. We acknowledge the generous assistance of Carrie Craig (Smithsonian Institution) and Mike Skinner (Pensoft) proofreading the manuscript. The following botanists kindly provided permission to use their pictures in this publication: Ching-I Peng (Academia Sinica, Taiwan; deceased), Forest and Kim Starr (Starr Environmental, Hawai'i), Jean-Yves Meyer (Délégation à la Recherche, Tahiti, French Polynesia & Tetiaroa Society), Karl Magnacca (Hawai'i) and Lawrence Jensen (University of Auckland, New Zealand). We are grateful to the following online resources and institutions for providing virtual access to specimens and literature: Biodiversity Heritage Library (BHL), Harvard University Herbaria (HUH), International Plant Names Index (IPNI), JSTOR Global Plants, Missouri Botanical Garden (MO), New York Botanical Garden (NY), Smithsonian Institution (US) and the Smithsonian's Flora of the Hawaiian Islands website.

References

Airy-Shaw HK (1952) On the distribution of *Pisonia grandis* R. Br. (Nyctaginaceae), with special reference to Malaysia. Kew Bulletin 7(1): 87–97. https://doi.org/10.2307/4117674

Bargagli-Petrucci G (1901) Le specie di *Pisonia* della regione di Monsoni. Nuovo Giornale Botanico Italiano 8: 603–625.

Beauvisage G (1901) Genera Montrouzierana, plantarum Nova Caledonieae. Annales de la Société Botanique de Lyon 26(2): 49–96. https://doi.org/10.3406/linly.1901.4713

Bentham G, Hooker JD (1880) Genera plantarum ad exemplaria imprimis in herbariis kewensibus servata definita, Vol. 3, pt. 1. Reeves & Co., London.

Burger AE (2005) Dispersal and germination of seeds of *Pisonia grandis*, an Indo-Pacific tropical tree associated with insular seabird colonies. Journal of Tropical Ecology 21(3): 263–271. https://doi.org/10.1017/S0266467404002159

Caraballo-Ortiz MA, Trejo-Torres JC (2017) Two new endemic tree species from Puerto Rico: *Pisonia horneae* and *Pisonia roqueae* (Nyctaginaceae). PhytoKeys 86: 97–115. https://doi.org/10.3897/phytokeys.86.11249

Choisy JD (1849) Nyctaginaceae. In: de Candolle A (Ed.) Prodromus Systematis Naturalis Regni Vegetabilis, Vol. 13, pt. 2. Masson, Paris, 425–458.

Douglas N, Spellenberg R (2010) A new tribal classification of Nyctaginaceae. Taxon 59(3): 905–910. https://doi.org/10.1002/tax.593018

Du Petit-Thouars LMA (1804) Histoire des végéteux recueillis sur les isles de France, La Réunion (Bourbon) et Madagascar. Huzard, Paris.

Du Petit-Thouars LMA (1806) Histoire des végéteux recueillis dans les Îsles Australes d'Afrique. Tourneisen, Paris. https://doi.org/10.5962/bhl.title.163949

Florence J (2004) Flore de la Polynésie Française, Vol. 2. Collection Faune et Flore tropicales 41. IRD Éditions, Publications Scientifiques du Muséum National D'Histoire Naturelle, Paris.

Forster JR, Forster G (1776) Characteres Generum Plantarum. B. White, T. Cadell, & P. Elmsly, London.

Fosberg FR (1987) A new *Pisonia* (Nyctaginaceae) from the Hawaiian Islands. Phytologia 62(3): 177–178.

Friedmann F (1986) Étude de la structure du périanthe chez des *Pisonia* paléotropicaux et description de *P. sechellarum* sp. nov. (Nyctaginaceae). Bulletin du Muséum National d'Histoire Naturelle. Section B. Adansonia 8(4): 383–392.

Hayward J, Hynson NA (2014) New evidence of ectomycorrhizal fungi in the Hawaiian Islands associated with the endemic host *Pisonia sandwicensis* (Nyctaginaceae). Fungal Ecology 12: 62–69. https://doi.org/10.1016/j.funeco.2014.09.001.

Heimerl A (1889) Nyctaginaceae. In: Engler A, Prantl K (Eds) Die Natürlichen Pflanzenfamilien, Vol. 1b. Engelmann, Leipzig, 14–32.

Heimerl A (1913a) Über die Nyctaginaceen-Gattung *Calpidia*. Österreichische Botanische Zeitschrift 63(1): 19–21. https://doi.org/10.1007/BF01640846

Heimerl A (1913b) Die Nyctaginaceen-Gattungen *Calpidia* und *Rockia*. Österreichische Botanische Zeitschrift 63(7): 279–290. https://doi.org/10.1007/BF01642830

Heimerl A (1934) Nyctaginaceae. In: Engler A, Harms H (Eds) Die Natürlichen Pflanzenfamilien, ed. 2, Vol. 16c. Engelmann, Leipzig, 86–134.

Heimerl A (1937) Nyctaginaceae of southeastern Polynesia and other Pacific islands. Occasional Papers of Bernice Pauahi Bishop Museum of Polynesian Ethology and Natural History 13(4): 27–47.

Merrill ED, Perry LM (1939) Plantae Papuanae Archboldianae, I. Journal of the Arnold Arboretum 20(3): 324–345.

Montrouzier JXH (1860) Flore de L'Île Art (près de la Nouvelle Calédonie). Mémoires de l'Académie Royale des Sciences, Belles Lettres et Arts de Lyon. Section des Sciences 10: 173–254.

Murphy S, Legge S (2003) A first record of a land-bird being trapped by *Pisonia umbellifera*. The Sunbird 33(3): 111–112.

Philcox D, Coode MJE (1994) Nyctaginacées (family 141). In: Bosser J, Cadet T, Guého J, Marais W (Eds) Flore des Mascareignes: La Réunion, Maurice, Rodrigues (136. Myoporacées à 148. Hydnoracées). The Sugar Industry Research Institute, Mauritius, ORSTOM, Paris & The Royal Botanic Gardens, Kew, 1–12.

Pramanick DD, Maiti GG, Mondal MS (2015) Taxonomic study of the genus *Pisonia* L. (Nyctaginaceae) in India. Annals of Plant Sciences 4(8): 1179–1185.

Rossetto EFS, Faria AD, Ruas PM, Ruas CF, Douglas NA, Ribeiro JELS (2019) Clarifying generic delimitation in Nyctaginaceae tribe Pisonieae after more than a century of taxonomy confusion. Botanical Journal of the Linnean Society 189(4): 378–396. https://doi.org/10.1093/botlinnean/boz001

Seemann B (1863) On the genus *Ceodes* of Forster. Journal of Botany, British and Foreign 1: 244–246.

Skottsberg C (1926) Vascular plants from the Hawaiian Islands. I. Acta Horti Gothoburgensis 2: 185–284.

Skottsberg C (1936) The arboreous Nyctaginaceae of Hawaii. Svensk Botanisk Tidskrift 30: 722–743.

Skottsberg C (1941) *Heimerliodendron* nov. nom. Svensk Botanisk Tidskrift 35: 364.

St. John H (1951) The distribution of *Pisonia grandis* (Nyctaginaceae). Webbia 8: 225–228. https://doi.org/10.1080/00837792.1951.10669600

Stemmerik JF (1964a) Flora Malesianae Precursores XXXVIII: Notes on *Pisonia* L. in the Old World (Nyctaginaceae). Blumea 12: 275–284.

Stemmerik JF (1964b) Nyctaginaceae. In: van Steenis CGGJ (Ed.) Flora Malesiana, Vol. 6. Wolters-Noordhoff Publishing, Groningen, 450–468.

Sykes WR (1987) The parapara, *Pisonia brunoniana* (Nyctaginaceae). New Zealand Journal of Botany 25(3): 459–466. https://doi.org/10.1080/0028825X.1987.10413362

von Höhnel FXR (1903) Mykologische Fragmente. Annales Mycologici 1(5): 391–414.

Wagner WL, Herbst DR, Lorence DH (2005) Flora of the Hawaiian Islands website. http://botany.si.edu/pacificislandbiodiversity/hawaiianflora/index.htm [accessed 03.15.2020]

Walker TA, Chaloupka MY, King BR (1991) *Pisonia* islands of the Great Barrier Reef, part 1. Atoll Research Bulletin 350: 1–23. https://doi.org/10.5479/si.00775630.350-1.1

Warburg O (1891) Beiträge zur Kenntnis der papuanischen Flora. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 13: 230–455.

Whistler WA (2004) Rainforest trees of Samoa: A guide to the common lowland and foothill forest trees of the Samoan Archipelago. Isle Botanica, Honolulu.