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A molecular phylogeny of *Boronia* (Rutaceae): placement of enigmatic taxa and a revised infrageneric classification

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ABSTRACT

A phylogeny of *Boronia* (Rutaceae) is presented on the basis of maximum parsimony and Bayesian analyses of plastid (*psb*A–*trn*H, *trn*L–*trn*F, *rbc*L) and nuclear (*ITS*, *ETS*) markers. Analyses of either plastid or nuclear sequences recovered the same major clades, although with conflicts in resolution among them. The existing classification of *Boronia* is largely confirmed; sections *Boronella*, *Pedunculatae* and *Valvatae* are supported, and the monotypic sections *Alatae* and *Imbricatae* are isolated. *Boronia corynophylla* Paul G.Wilson is removed from section *Algidae* to the new section *Corynophyllae*. *Boronia coriacea* Paul G.Wilson is removed from section *Boronia* and placed, with *B. inornata* Turcz., in the new section *Inornatae*. *Boronia humifusa* Paul G.Wilson, *B. ovata* Lindl. and *B. scabra* Lindl. are placed in the new section *Ovatae*. *Boronia koniambiensis* is retained in section *Boronella* but placed in a new monotypic series. Section *Boronia* resolves into two clades that are confined to either south-eastern or south-western Australia, the latter containing three strongly to robustly supported subclades. An identified problem within section *Boronia* is the lack of morphological apomorphies to assist with formal classification. Despite this, a classification of four series, justified on the basis of the results of the molecular analysis, is proposed. Relationships among the 10 sections of *Boronia* remain poorly resolved apart from the sister relationships of sections *Imbricatae* with *Pedunculatae*, and, *Alatae* with *Corynophyllae*.

Keywords: Australasia, *Boronia*, molecular phylogenetics, moth pollination, plant systematics, Rutaceae, taxonomy.

Introduction

Boronia Sm. (Rutaceae) is an Australian and New Caledonian genus of 134 species comprising mainly shrubs but also occasionally small trees or subshrubs (Wilson 1971, 1998; Duretto 1999, 2003; Duretto *et al.* 2013, 2020; Bayly *et al.* 2015). The genus is taxonomically isolated in subfamily Zanthoxyloideae A.Juss. ex Arn. and is sister to a large clade containing genera found mainly in the Australasian–Malesian region, including those found in rainforest, for example, *Acronychia* J.R.Forst. & G.Forst., *Euodia* J.R.Forst. & G.Forst. and *Melicope* J.R.Forst. & G.Forst., and sclerophyllous communities, e.g. *Cyanothamnus* Lindl., *Neobyrnesia* J.A.Armstr. and *Zieria* Sm. (see Groppo *et al.* 2008; Bayly *et al.* 2013, 2015; Duretto *et al.* 2020; Appelhans *et al.* 2021).

There have been several infrageneric classifications proposed for *Boronia* over the past 150 years with most of the differences between classifications centred on taxa now placed in section *Boronia* or *incertae sedis* (i.e. uncertain placement) at the sectional level (Bayly *et al.* 2015; Duretto *et al.* 2020). Bayly *et al.* (2015) presented a phylogenetic analysis using molecular data and demonstrated that *Boronella* Baill. was nested in *Boronia* and, apart from section *Boronia*, all sections recognised for the genus *Boronia* in recent treatments were monophyletic or, if monotypic, then divergent from other sections, separated on relatively long terminal branches. They also showed that both section *Boronia* and series *Boronia* were polyphyletic. Bayly *et al.* (2015) circumscribed section *Boronia* in a stricter sense with no series, reduced *Boronella* to a section of *Boronia*, raised series *Pedunculatae* Benth. (previously placed in section *Boronia*) to sectional level and placed as *incertae sedis* (at the sectional level) four species, *B. humifusa* Paul G.Wilson, *B. inornata* Turcz., *B. ovata* Lindl. and *B. scabra* Lindl., that had been placed in series *Boronia* (Wilson 1998; Duretto 2003; Duretto *et al.* 2013). Bayly *et al.* (2015) also placed *Boronia* series *Ovatae* Paul G.Wilson as *incertae sedis*. This last series was formally described by Wilson (1971; under section *Imbricatae* Engl.) to accommodate *B. ovata* and *B. scabra*, although later he placed it in synonymy under series *Boronia* (Wilson 1998). Wilson (1998) also formally described *B. humifusa* and noted that the species was difficult to place although being similar to *B. ovata* and *B. scabra* in inflorescence characters.

Duretto *et al.* (2020) tested the monophyly of *Boronia* and demonstrated that *Boronia* (*sensu* Wilson 1971, 1998; Duretto 2003; Kubitzki *et al.* 2011; Duretto *et al.* 2013; Bayly *et al.* 2015) was polyphyletic and that section *Cyanothamnus* (Lindl.) F.Muell. was misclassified in *Boronia* and was more closely related to a large clade of genera found in rainforest, including *Melicope* and *Acronychia*. They reinstated the genus *Cyanothamnus*, with 23 species placed in six series.

In addition to the four *incertae sedis* species in *Boronia*, there are three other species, *B. coriacea* Paul G.Wilson (section *Boronia*), *B. corynophylla* Paul G.Wilson (section *Algidae* Duretto) and *B. koniambiensis* Däniker (section *Boronella* (Baill.) Duretto & Bayly), that are unusual morphologically, and their current taxonomic placement requires testing. The first two species have not been included in any phylogenetic analyses.

Boronia coriacea is a poorly collected and rare species from south-western Australia (SW Austr.). Wilson (1971), who described the species, and Duretto *et al.* (2013), in the *Flora of Australia*, did not discuss possible relationships of the species. Bayly *et al.* (2015) indicated that *B. coriacea* might be related to *B. inornata*, although critical morphological features, such as seeds, had not been described and were not available for study and, so, they retained it in section *Boronia*.

Boronia corynophylla was placed in section *Valvatae* (Benth.) Engl. when described by Wilson (1998) because it had valvate petals. Later Duretto (1999) moved it to the newly described section *Algidae* on the basis of it having sheathing and brown prophylls, imbricate sepals, valvate petals, and a terminal inflorescence of 1(–3) flowers. *Boronia corynophylla* differs from the other two species in section *Algidae* in having an exfoliating cuticle on its branches, simple, terete leaves and a small stigma.

Boronia koniambiensis was included in a cladistic analysis on the basis of morphological data presented by Weston *et al.* (1984) who resolved it as sister to the remainder of the species placed in the genus *Boronella* (≡*Boronia* section *Boronella*). The species is morphologically distinct from the other species of section *Boronella* in having glabrous branches (*v.* branches with tufts of simple hairs in the axils of the leaves), opposite decussate leaves (*v.* verticillate), an inflorescence that is a large cymose panicle (*v.* a pseudo-umbel), and valvate petals (*v.* imbricate; Hartley 1995; Bayly *et al.* 2015).

In *Boronia*, only section *Valvatae* has a formal infrasectional classification (Duretto and Ladiges 1998; Duretto 1999, 2008; Duretto *et al.* 2013), although this has not been tested using molecular data. Of the sections not discussed above, the following three do not have issues regarding monophyly: *Alatae* Duretto and *Imbricatae* are monotypic, and *Pedunculatae* (Benth.) Duretto & Bayly (11 spp.) is well-defined morphologically (Bayly *et al.* 2015). By contrast, section *Boronia* (23 spp.) is diverse morphologically, and the relationships of the species are unresolved even though several infrageneric taxa have been described to accommodate some of the more unusual taxa (Bayly *et al.* 2015). Many of the unusual morphological features found in the section are that of inflorescence and flower structures and appear to be associated with specialised host and pollination associations with day moths of the family Heliozelidae (Milla *et al.* 2018; Milla 2019; Wild 2022; L. Milla, A. Young, A. Mousalli, S. Wilcox, M. F. Duretto, M. F. Halsey, T. M. Jones, A. Kallies and D. J. Hilton, in prep.).

The relationships of the seven sections of *Boronia* and seven species of uncertain affinity are still not adequately understood. In both of the analyses presented by Bayly *et al.* (2015) and Duretto *et al.* (2020), there was strong support for sections *Imbricatae* and *Pedunculatae* being sister, and weaker support for a sister relationship between *B. inornata* and section *Alatae*, *B. scabra* with section *Boronia*, and this last clade with section *Boronella*.

The aims of the current study are to determine: (1) the relationships of the four species, *viz. B. humifusa, B. inornata, B. ovata* and *B. scabra*, and series *Ovatae* that were *incertae sedis* in Bayly *et al.* (2015), and *B. coriacea* (section *Boronia*), *B. corynophylla* (section *Algidae*) and *B. koniambiensis* (section *Boronella*); (2) the relationships of species placed in section *Boronia*; and (3) the relationships of the sections of *Boronia*. As with Duretto *et al.* (2020), three plastid markers (*psb*A–*trn*H, *trn*L–*trn*F and *rbc*L) and two nuclear ribosomal DNA markers (*ITS* and *ETS*) were used to construct robust molecular phylogenies to assess these relationships.

Materials and methods

Taxon sampling

Our dataset comprised 143 accessions of 85 species belonging to 8 genera from subfamily Zanthoxyloideae (see Appelhans *et al.* 2021); most are newly sequenced specimens, supplemented with samples from previously published studies (Table 1). The ingroup sits within clade D of Bayly *et al.* (2013, fig. 3) and the outgroups were chosen to represent other subclades within clade D, rooted with *Phebalium* to represent clade C of Bayly *et al.* (2013, fig. 3).

For the ingroup, 136 accessions of 78 species of *Boronia* were sampled from all 7 currently recognised sections

Table 1. Voucher details and GenBank accession numbers of taxa sampled.

Taxon	Section	Locality	Collector and number	Herbarium voucher	*ETS*	*ITS*	*trn*L–F	*psb*A–*trn*H	*rbc*L
Outgroup									
Acronychia baeuerlenii		Australia, NSW	M. Rossetto ABNIG1	NSW	LN849223	LN849139	LN849180	LN849162	–
Cyanothamnus anemonifolius subsp. *anemonifolius*		Australia, NSW	S. Rutherford 157	NSW 971602	MN082812	MN082859	MN082997	MN082943	MN083038
Cyanothamnus polygalifolius		Australia, cult. BMBG, ex NSW	M.F. Duretto 3051a	NSW 1057660	MN082822	MN082869	MN083007	MN082957	MN083039
Euodia hylandii		Australia, Qld	P.I. Forster 25754	MEL 2115620A	HG971479	HG971326	HG971169	HG971042	–
Medicosma fareana		Australia, Qld	K. Hill 2095	NSW 200414	MN082835	MN082882	MN083020	MN082973	MN083046
Phebalium canaliculatum		Australia, WA	M.J. Bayly 2457	NSW 1058468	MN082843	MN082888	MN083028	MN082981	MN083051
Zieria arborescens subsp. *arborescens*		Australia, Vic.	M.J. Bayly 1868	MELU 120871	KP867748	KP867675	KP188949	–	JN987143
Ingroup									
Boronia alata	*Alatae*	Australia, WA, Leeuwin Naturaliste NP	M.J. Bayly 1955	MEL 2383602A	KP867734	KP867656	KP867809	MN082896	–
Boronia albiflora	*Boronia*	Australia, WA, Condingup	G. Byrne 2600	PERTH 7958552	**OP654199**	**OP653792**	**OP654391**	**OP654298**	–
Boronia albiflora	*Boronia*	Australia, WA, Fitzgerald River NP	M Crowhurst 39	PERTH 8249962	**OP654200**	–	–	**OP654299**	–
Boronia albiflora	*Boronia*	Australia, WA, Stirling Range NP	D.A. Young V#18	NSW 1006021	**OP654201**	**OP653793**	**OP654392**	**OP654300**	–
Boronia algida	*Algidae*	Australia, Vic., Mount Buffalo NP	M.J. Bayly 1958	MEL 2383605	KP867742	KP867677	KP867779	MN082897	–
Boronia algida	*Algidae*	Australia, NSW, Blue Mountains	G. Bourke 69	NSW	**OP654202**	**OP653794**	**OP654393**	**OP654301**	**OP654292**
Boronia algida	*Algidae*	Australia, NSW, Gibraltar Range NP	M.A.M. Renner 6739	NSW 881132	**OP654203**	**OP653795**	**OP654394**	**OP654302**	–
Boronia alulata	*Valvatae*	Australia, Qld, Richardson Range	P.I. Forster 33637	BRI AQ0743487	KP867724	KP867696	KP867793	MN082898	–

(*Continued on next page*)

Table 1. (*Continued*)

Taxon	Section	Locality	Collector and number	Herbarium voucher	*ETS*	*ITS*	*trn*L–F	*psb*A–*trn*H	*rbc*L
Boronia angustisepala	*Valvatae*	Australia, NSW, Mount Kaputar NP	K. Durham *s.n.*	NSW 977045	**OP654204**	**OP653796**	–	**OP654303**	–
Boronia barkeriana subsp. *angustifolia*	*Pedunculatae*	Australia, Tianjara Falls, NSW	F. Howe SH/599	CBG 7707632.1	**OP654205**	**OP653797**	**OP654395**	**OP654304**	–
Boronia barkeriana subsp. *angustifolia*	*Pedunculatae*	Australia, NSW, Morton NP	M.F. Duretto 3114	NSW 1005445	**OP654206**	**OP653798**	**OP654396**	**OP654305**	–
Boronia barkeriana subsp. *barkeriana*	*Pedunculatae*	Australia, NSW, Blue Mountains NP	M. Elgey 41	NSW 926860	**OP654207**	**OP653799**	**OP654397**	**OP654306**	–
Boronia barkeriana subsp. *barkeriana*	*Pedunculatae*	Australia, NSW, cult. BMBG, ex Mount Wilson	M.F. Duretto 3086A	NSW 1058627	**OP654208**	**OP653800**	**OP654398**	**OP654307**	**OP654293**
Boronia bowmanii	*Valvatae*	Australia, Qld, Shelburne Bay (Nixon) homestead	P.I. Forster 33638	BRI AQ0743488	KP867723	KP867692	KP867760	MN082899	–
Boronia capitata subsp. *capitata*	*Boronia*	Australia, WA, North Tarin Rock NR	T. Nicholls 4924	PERTH 7821573	**OP654209**	**OP653801**	**OP654399**	**OP654308**	–
Boronia capitata subsp. *gracilis*	*Boronia*	Australia, WA, (sensitive)	P.Foreman, G.Smith NR582	PERTH 8277079	**OP654210**	**OP653802**	**OP654400**	**OP654309**	–
Boronia capitata subsp. *gracilis*	*Boronia*	Australia, WA, (sensitive)	D.A. Young V#35	NSW 1006054	**OP654211**	**OP653803**	**OP654401**	**OP654310**	–
Boronia citriodora subsp. *citriodora*	*Boronia*	Australia, Tas., Mount Field NP	M.F. Duretto 3511	NSW 1005469	**OP654212**	**OP653804**	**OP654402**	**OP654311**	–
Boronia citriodora subsp. *citriodora*	*Boronia*	Australia, Tas., Cradle Mountain–Lake St Clair NP	M.F. Duretto 2244	NSW 1057657	KP867709	KP867697	KP867806	–	–
Boronia citriodora subsp. *paulwilsonii*	*Boronia*	Australia, Tas., The Needles	M.F. Duretto 3510	NSW 1005468	**OP654213**	**OP653805**	**OP654403**	**OP654312**	–
Boronia clavata	*Boronia*	Australia, WA, (sensitive)	G. Warden-Johnson, K.Gonnar AR314	PERTH 8311919	**OP654214**	–	**OP654404**	**OP654313**	–
Boronia clavata	*Boronia*	Australia, WA, (sensitive)	E. Massenbauer 705 #1	NSW 992151	**OP654215**	**OP653806**	**OP654405**	**OP654314**	–
Boronia corynophylla	*Corynophyllae*	Australia, WA, (sensitive)	P. Armstrong PA06/234	PERTH 7883943	**OP654216**	–	–	**OP654315**	–
Boronia crassifolia	*Boronia*	Australia, WA, Jerramungup	G. Byrnes 3985, 08sep10	PERTH 8296820	**OP654217**	**OP653807**	**OP654406**	**OP654316**	–

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Table 1. (*Continued*)

Taxon	Section	Locality	Collector and number	Herbarium voucher	*ETS*	*ITS*	*trn*L–F	*psb*A–*trn*H	*rbc*L
Boronia crassifolia	*Boronia*	Australia, WA, South Stirlings	D.A. Young 8.9.2015	NSW 992139	**OP654218**	**OP653808**	**OP654407**	**OP654317**	–
Boronia crassipes	*Boronia*	Australia, WA, (sensitive)	S. Barrett 2067	PERTH 8329672	**OP654219**	**OP653809**	**OP654408**	**OP654318**	–
Boronia crenulata	*Boronia*	Australia, WA, Boat Harbour Rd	M.J. Bayly 1957	MEL 2383610A	KP867740	KP867660	KP867788	MN082900	–
Boronia crenulata subsp. *crenulata*	*Boronia*	Australia, cult. ANBG, ex Cheyne Beach, WA	J. Armstrong 5048	CBG 8306143.1	**OP654220**	**OP653810**	**OP654409**	**OP654319**	–
Boronia crenulata subsp. *pubescens*	*Boronia*	Australia, WA, Cundinup West	D.A. Young *s.n.*	NSW 992168	**OP654221**	**OP653811**	–	**OP654320**	–
Boronia crenulata subsp. *viminea*	*Boronia*	Australia, WA, Stirling Range NP	D.A. Young V#19	NSW 1006061	**OP654222**	**OP653812**	**OP654410**	**OP654321**	–
Boronia cymosa	*Imbricatae*	Australia, WA, SE of Eneabba	M.J. Bayly 1906	MEL 2383604A	KP867729	KP867684	KP867771	MN082901	MW840275
Boronia deanei subsp. *acutifolia*	*Boronia*	Australia, cult. ANBG, ex Fitzroy Falls, NSW	M.J. Bayly 2001	MELU 105858	KP867733	KP867704	KP867795	MN082902	–
Boronia deanei subsp. *deanei*	*Boronia*	Australia, NSW, Newnes SF	J. Cohen 14	NSW 853312	**OP654223**	**OP653813**	**OP654411**	**OP654322**	–
Boronia denticulata	*Pedunculatae*	Australia, cult. ANBG, ex Cheyne Beach, WA	J. Armstrong 5050	CBG 8306145.1	**OP654224**	**OP653814**	**OP654412**	**OP654323**	–
Boronia denticulata	*Pedunculatae*	Australia, WA, Granite Hill Reserve	D.A. Young *s.n.*	NSW 992177	**OP654225**	**OP653815**	–	**OP654324**	–
Boronia dichotoma	*Pedunculatae*	Australia, cult. ANBG, ex Bunbury–Mandurah, WA	J.W. Wrigley WA/68 4735	CBG 36718.1	**OP654226**	**OP653816**	**OP654413**	**OP654325**	–
Boronia edwardsii	*Algidae*	Australia, SA, Fleurieu Peninsula	M.J. Bayly 1974	MEL 2383596A	KP867744	KP867694	KP867786	MN082904	–
Boronia elisabethiae	*Boronia*	Australia, Tas., Lake Peddar Rd	M.F. Duretto 3508	NSW 1005466	**OP654227**	**OP653817**	**OP654414**	**OP654326**	–
Boronia excelsa	*Valvatae*	Australia, Qld, Mount Windsor NP	P.I. Forster 34665	BRI AQ745462	KP867752	KP867659	KP867810	MN082905	–
Boronia falcifolia	*Boronia*	Australia, Qld, Great Sandy NP	P.I. Forster 34199	BRI AQ0743521	KP867754	KP867678	KP867801	MN082906	–
Boronia falcifolia	*Boronia*	Australia, Qld, Doonan	T. Wilson 499	NSW 978686	**OP654228**	**OP653818**	**OP654415**	**OP654327**	**OP654294**

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Table 1. (*Continued*)

Taxon	Section	Locality	Collector and number	Herbarium voucher	*ETS*	*ITS*	*trn*L–F	*psb*A–*trn*H	*rbc*L
Boronia falcifolia	*Boronia*	Australia, NSW, Yuraygir NP	M.F. Duretto 3527	NSW 1005482	**OP654229**	**OP653819**	**OP654416**	**OP654328**	–
Boronia filifolia	*Boronia*	Australia, SA, Fleurieu Peninsula	M.J. Bayly 1977	MEL 2383598A	KP867722	KP867654	KP867767	MN082907	–
Boronia floribunda	*Boronia*	Australia, NSW, Berowra Valley NP	M.F. Duretto 3007	NSW 1005407	KP867730	KP867671	KP867811	MN082908	–
Boronia forsteri	*Valvatae*	Australia, Qld, Expedition NP	T. Wilson 484	NSW 978682	**OP654230**	**OP653820**	**OP654417**	**OP654329**	–
Boronia fraseri	*Valvatae*	Australia, NSW, Ku-ring-gai Chase NP	M.F. Duretto 3078	NSW 1005426	**OP654231**	**OP653821**	**OP654418**	**OP654330**	–
Boronia galbraithiae	*Boronia*	Australia, Vic., Biragolong SF	M.J. Bayly 2031	MELU	**OP654232**	MN082852	MN082990	MN082909	–
Boronia glabra	*Valvatae*	Australia, Qld, Millmerran Woods	A. Orme 1065	NSW 590112	**OP654233**	**OP653822**	**OP654419**	**OP654331**	–
Boronia gracilipes	*Boronia*	Australia, cult. ANBG, ex Valley of the Giants, WA	M.J. Bayly 2003	MELU 105859	KP867735	KP867669	KP867774	MN082910	–
Boronia granitica	*Valvatae*	Australia, Qld, Passchendaele SF	M.T. Mathieson 259	BRI AQ0745449	KP867731	KP867680	KP867764	MN082911	–
Boronia gunnii	*Boronia*	Australia, cult. ANBG, ex Denison Riverlet, Tas.	R. Burns ANBG 1411	CBG 8701905.1	**OP654234**	**OP653823**	**OP654420**	**OP654332**	–
Boronia gunnii	*Boronia*	Australia, Tas., St Pauls River	M.F. Duretto 2056	MEL 2308868A	**OP654235**	**OP653824**	–	**OP654333**	–
Boronia hemichiton	*Boronia*	Australia, Tas., Ben Lomond	M.F. Duretto 1962	NSW 832370	**OP654236**	**OP653825**	–	**OP654334**	–
Boronia heterophylla	*Boronia*	Australia, cult. ANBG, ex WA (provenance unknown)	M.J. Bayly 2004	MELU 105860	KP867736	KP867657	KP867775	MN082912	–
Boronia heterophylla	*Boronia*	Australia, WA, Nannup	D.A. Young *s.n.*	NSW 992169	**OP654237**	**OP653826**	–	**OP654335**	–
Boronia heterophylla	*Boronia*	Australia, WA, Millbrook NR	D.A. Young V#20	NSW 1006029	**OP654238**	**OP653827**	**OP654421**	**OP654336**	MW840274
Boronia hippopala	*Boronia*	Australia, Tas., Meadstone Falls Rd	M.F. Duretto 2027	NSW 832372	**OP654239**	**OP653828**	–	**OP654337**	–
Boronia humifusa	*Ovatae*	Australia, WA, (sensitive)	E. Bennett 02/5	PERTH 8001766	**OP654240**	**OP653829**	–	**OP654338**	–

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Table 1. (*Continued*)

Taxon	Section	Locality	Collector and number	Herbarium voucher	*ETS*	*ITS*	*trn*L–F	*psb*A–*trn*H	*rbc*L
Boronia imlayensis	*Boronia*	Australia, NSW, Mount Imlay	M.J. Bayly 2005	MELU 105861	KP867728	KP867652	KP867776	MN082913	–
Boronia imlayensis	*Boronia*	Australia, NSW, Mount Imlay	G. Errington 812	NSW 885702	**OP654241**	**OP653830**	**OP654422**	**OP654339**	–
Boronia imlayensis	*Boronia*	Australia, NSW, Mount Imlay	S. Pedersen 772	CANB 662843	**OP654242**	**OP653831**	**OP654423**	**OP654340**	–
Boronia inornata	*Inornatae*	Australia, WA, Lake King-Ravensthorpe Road	M.J. Bayly 1947	MEL 2383608A	KP867719	KP867688	KP867773	MN082914	–
Boronia inornata subsp. *inornata*	*Inornatae*	Australia, WA, Hopetoun	D.A. Young *s.n.*	NSW 992142	**OP654243**	**OP653832**	**OP654424**	**OP654341**	–
Boronia inornata subsp. *leptophylla*	*Inornatae*	Australia, WA, Breakaway Ridge Reserve	G. Byrne 3928	NSW 929015	**OP654244**	**OP653833**	–	**OP654342**	–
Boronia inornata subsp. *leptophylla*	*Inornatae*	Australia, SA, Hundred of Playford, Cowell	R. Taylor 1049	AD 208016	**OP654245**	**OP653834**	**OP654425**	**OP654343**	–
Boronia inornata subsp. *leptophylla*	*Inornatae*	Australia, SA, Heggaton CP	D.J. Duval 904	AD 214838	**OP654246**	**OP653835**	**OP654426**	**OP654344**	–
Boronia inornata subsp. *leptophylla*	*Inornatae*	Australia, WA, Ravensthorpe Range	D.A. Young V#23	NSW 1006049	**OP654247**	**OP653836**	–	**OP654345**	–
Boronia keysii	*Valvatae*	Australia, Qld, Cooloola NP	M.T. Mathieson 281	BRI AQ0746001	KP867713	KP867689	KP867770	MN082915	–
Boronia koniambiensis	*Boronella*	New Caledonia, Grande Terre	M.F. Duretto 1403	HO 561946	**OP654248**	**OP653837**	**OP654427**	**OP654346**	**OP654295**
Boronia koniambiensis	*Boronella*	New Caledonia, Grande Terre	M.F. Duretto 1404	HO 561947	**OP654249**	**OP653838**	**OP654428**	**OP654347**	–
Boronia lanceolata	*Valvatae*	Australia, NT, Nitmiluk NP	M.F. Duretto 532	MEL 2042755A	KP867732	KP867679	KP867790	MN082916	–
Boronia lanuginosa	*Valvatae*	Australia, NT, Nitmiluk NP	M.F. Duretto 1243	MELU	KP867715	KP867691	KP867785	–	–
Boronia latipinna	*Boronia*	Australia, Vic., Grampians NP	M.J. Bayly 1983	MEL 2383593A	KP867749	KP867666	KP867794	MN082917	–
Boronia ledifolia	*Valvatae*	Australia, NSW, Berowra Valley NP	M.F. Duretto 3006	NSW 1005406	KP867758	KP867700	KP867781	MN082918	–
Boronia megastigma	*Boronia*	Australia, WA, Cobertup Reserve	D.A. Young V#27	NSW 1006046	**OP654250**	**OP653839**	**OP654429**	**OP654348**	–

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Table 1. (*Continued*)

Taxon	Section	Locality	Collector and number	Herbarium voucher	*ETS*	*ITS*	*trn*L–F	*psb*A–*trn*H	*rbc*L
Boronia megastigma	*Boronia*	Australia, WA, Porongurup Range	D.A. Young V#26	NSW 1006062	**OP654251**	**OP653840**	**OP654430**	**OP654349**	–
Boronia megastigma	*Boronia*	Australia, WA, Collie	D.A. Young V#52	NSW 1006041	**OP654252**	**OP653841**	**OP654431**	**OP654350**	–
Boronia megastigma	*Boronia*	Australia, WA, Witchcliffe	G.J. Keighery 15979	PERTH 6252931	**OP654253**	**OP653842**	**OP654432**	**OP654351**	–
Boronia microphylla	*Boronia*	Australia, NSW, Newnes SF	P. Hind 6706	NSW 406248	KP867755	KP867683	KP867787	MN082919	**OP654296**
Boronia microphylla	*Boronia*	Australia, NSW, Gibraltar Range	G. Bourke 70	NSW	**OP654254**	**OP653843**	**OP654433**	**OP654352**	–
Boronia microphylla	*Boronia*	Australia, NSW, Bonnie Doon Reserve	M.F. Duretto 3070	NSW 1005419	**OP654255**	**OP653844**	**OP654434**	**OP654353**	–
Boronia molloyae	*Boronia*	Australia, WA, Cundinup West	D.A. Young *s.n.*	NSW 992171	**OP654256**	**OP653845**	**OP654435**	**OP654354**	–
Boronia molloyae	*Boronia*	Australia, cult. ANBG, ex Manjimup, WA	J. Armstrong 5060	CBG 8306155.1	**OP654257**	**OP653846**	**OP654436**	**OP654355**	–
Boronia muelleri	*Boronia*	Australia, Vic., Bunyip State Park	M.J. Bayly 1968	MELU 120564a	–	KP867665	KP867803	MN082920	–
Boronia muelleri	*Boronia*	Australia, cult. ANBG, ex Wingan Inlet, Vic.	M.E. Phillips 180	CBG 7409.1	**OP654258**	**OP653847**	**OP654437**	**OP654356**	–
Boronia nematophylla	*Boronia*	Australia, WA, Lake Muir	D.A. Young V#38	NSW 1006036	**OP654259**	**OP653848**	**OP654438**	**OP654357**	–
Boronia obovata	*Valvatae*	Australia, Qld, Blackdown Tableland NP	T. Wilson 493	NSW 978684	**OP654260**	**OP653849**	**OP654439**	**OP654358**	–
Boronia octandra	*Boronia*	Australia, WA, Breakaway Ridge Reserve	G. Byrne 3940	PERTH 8296766	**OP654261**	**OP653850**	–	**OP654359**	–
Boronia octandra	*Boronia*	Australia, WA, Ravensthorpe	D.A. Young *s.n.*	NSW 992143	**OP654262**	**OP653851**	**OP654440**	**OP654360**	–
Boronia ovata	*Ovatae*	Australia, WA, Mundaring	K.R.Thiele 2111	PERTH 7890966	**OP654263**	**OP653852**	–	**OP654361**	–
Boronia oxyantha var. *brevicalyx*	*Boronia*	Australia, WA, Ravensthorpe	D.A. Young *s.n.*	NSW 992145	**OP654264**	**OP653853**	**OP654441**	**OP654362**	–
Boronia oxyantha var. *brevicalyx*	*Boronia*	Australia, WA, Ravensthorpe	M. Bennett 897	PERTH 6956661	**OP654265**	**OP653854**	**OP654442**	**OP654363**	–
Boronia pancheri	*Boronella*	New Caledonia, Grande Terre	M.J. Bayly 2046	MEL 2383623A	KP867739	KP867682	KP867784	MN082921	JN987078

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Table 1. (*Continued*)

Taxon	Section	Locality	Collector and number	Herbarium voucher	*ETS*	*ITS*	*trn*L–F	*psb*A–*trn*H	*rbc*L
Boronia pancheri	*Boronella*	New Caledonia, Grande Terre	M.F. Duretto 1413	HO 561633	**OP654266**	**OP653855**	**OP654443**	**OP654364**	**OP654297**
Boronia parviflora	*Pedunculatae*	Australia, Tas., Freycinet NP	M.F. Duretto 3518	NSW 1005476	**OP654267**	**OP653856**	**OP654444**	**OP654365**	–
Boronia parviflora	*Pedunculatae*	Australia, Tas., Tasman Peninsula	M.F. Duretto 2238	HO 561573	KP867727	KP867651	KP867780	–	–
Boronia parvifolia	*Boronella*	New Caledonia, Grande Terre	M.J. Bayly 2047	MEL 2383624A	KP867741	KP867673	KP867762	MN082922	JN987077
Boronia parvifolia	*Boronella*	New Caledonia, Grande Terre	M.J. Bayly 2115	MEL 2383638A	KP867750	KP867662	KP867783	MN082923	–
Boronia parvifolia	*Boronella*	New Caledonia, Grande Terre	M.F. Duretto 1410	HO 561948	**OP654268**	**OP653857**	**OP654445**	**OP654366**	–
Boronia pilosa subsp. *parvidaemonis*	*Boronia*	Australia, Vic., Little Desert NP	A. Carle 132	MEL 2365863A	**OP654269**	**OP653858**	**OP654446**	**OP654367**	–
Boronia pilosa subsp. *pilosa*	*Boronia*	Australia, Tas., Freycinet NP	M.F. Duretto 3517	NSW 1005475	**OP654270**	**OP653859**	**OP654447**	**OP654368**	–
Boronia pilosa subsp. *pilosa*	*Boronia*	Australia, Tas., Coles Bay	M.F. Duretto 3521	NSW 1005479	**OP654271**	**OP653860**	**OP654448**	**OP654369**	–
Boronia pilosa subsp. *pilosa*	*Boronia*	Australia, Vic., Lerderderg State Park	N.G. Walsh 6996	MEL 2328899A	**OP654272**	**OP653861**	**OP654449**	**OP654370**	–
Boronia pilosa subsp. *pilosa*	*Boronia*	Australia, Vic., Grampians NP	M.J. Bayly 1984	MEL 2383590A	**OP654273**	**OP653862**	**OP654450**	**OP654371**	–
Boronia pilosa subsp. *pilosa*	*Boronia*	Australia, Tas., Chimney Pot Hill	M.F. Duretto 2126	HO 549436	KP867746	KP867648	KP867766	MN082924	–
Boronia pilosa subsp. *tasmanensis*	*Boronia*	Australia, Tas., Tasman NP	M.F. Duretto 3515	NSW 1005473	**OP654274**	–	**OP654451**	**OP654372**	–
Boronia pilosa subsp. *torquata*	*Boronia*	Australia, Vic., Mount Richmond NP	M.F. Duretto 1526	MEL 2068652A	–	**OP653863**	–	**OP654373**	–
Boronia pinnata	*Boronia*	Australia, NSW, Ku-Ring-Gai Chase NP	M.F. Duretto 3005	NSW 1006082	KP867720	KP867672	KP867798	MN082925	–
Boronia pulchella	*Boronia*	Australia, WA, Stirling Range NP	D.A. Young *s.n.*	NSW 992167	**OP654275**	**OP653864**	**OP654452**	**OP654374**	–

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Table 1. (*Continued*)

Taxon	Section	Locality	Collector and number	Herbarium voucher	*ETS*	*ITS*	*trn*L–F	*psb*A–*trn*H	*rbc*L
Boronia purdieana subsp. *calcicola*	*Boronia*	Australia, WA, S of Kalbarri	D.A. Young *s.n.*	NSW 992175	**OP654276**	**OP653865**	**OP654453**	**OP654375**	–
Boronia purdieana subsp. *calcicola*	*Boronia*	Australia, WA, Kalbarri NP	D.A. Young *s.n.*	NSW 992176	**OP654277**	**OP653866**	**OP654454**	**OP654376**	–
Boronia repanda	*Valvatae*	Australia, Qld, Stanthorpe	M.T. Mathieson 201	BRI AQ0745476	KP867721	KP867649	KP867807	MN082926	–
Boronia rhomboidea	*Boronia*	Australia, Tas., Cradle Mountain-Lake St Clair NP	M.F. Duretto 2245	NSW 1057658	KP867708	KP867695	KP867797	MN082927	–
Boronia rivularis	*Boronia*	Australia, Qld, Maryborough-Tuan Forest Road	G. Thomas PC3	BRI AQ0757152	**OP654278**	**OP653867**	**OP654455**	**OP654377**	–
Boronia rivularis	*Boronia*	Australia, Qld, Cooloola NP	M.T. Mathieson 279	BRI AQ0745999	–	KP867687	KP867789	MN082928	–
Boronia rosmarinifolia	*Valvatae*	Australia, Qld, Great Sandy NP	P.I. Forster 34191	BRI AQ0743519	KP867751	KP867685	KP867763	MN082929	–
Boronia rosmarinifolia	*Valvatae*	Australia, Qld, Hilliards Creek Reserve	M.F. Duretto 3077	NSW 1005425	**OP654279**	**OP653868**	**OP654456**	**OP654378**	–
Boronia ruppii	*Valvatae*	Australia, cult. BMBG, ex Woodsreef, NSW	M.F. Duretto 3084	NSW 1058538	**OP654280**	**OP653869**	**OP654457**	**OP654379**	–
Boronia safrolifera	*Boronia*	Australia, NSW, Yuraygir NP	M.F. Duretto 3528	NSW 1005483	**OP654281**	**OP653870**	**OP654458**	**OP654380**	–
Boronia scabra	*Ovatae*	Australia, WA, Young River	M.J. Bayly 1946	MEL 2383611A	KP867737	KP867663	KP867799	MN082931	JN987079
Boronia scabra subsp. *scabra*	*Ovatae*	Australia, WA, Ravensthorpe Range	D.A. Young V#21	NSW 1006050	**OP654282**	**OP653871**	–	**OP654381**	–
Boronia serrulata	*Boronia*	Australia, NSW, Royal NP	A.N. Rodd 5623	NSW 196291	KP867759	KP867693	KP867804	MN082932	–
Boronia serrulata	*Boronia*	Australia, NSW, Ku-ring-gai Chase NP	M.F. Duretto 3529	NSW 1005485	**OP654283**	**OP653872**	**OP654459**	**OP654382**	–
Boronia sp. (as *Boronella* sp.)	*Boronella*	New Caledonia, Grande Terre	Lowry 6481	MO 1058022	HG971469	HG971314	HG971285	–	HG971621
Boronia spathulata	*Pedunculatae*	Australia, WA, Duke of Orleans Bay	M.J. Bayly 1945	MEL 2383607A	KP867757	KP867681	KP867768	MN082933	–
Boronia spathulata	*Pedunculatae*	Australia, WA, Lake Magenta Nature Reserve	A. Coates 5386	NSW 929017	**OP654284**	**OP653873**	**OP654460**	**OP654383**	–

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Table 1. (*Continued*)

Taxon	Section	Locality	Collector and number	Herbarium voucher	*ETS*	*ITS*	*trn*L–F	*psb*A–*trn*H	*rbc*L
Boronia splendida	*Valvatae*	Australia, Qld, Triumph Ck (Comet)	T. Wilson 488	NSW 978683	**OP654285**	**OP653874**	**OP654461**	**OP654384**	–
Boronia squamipetala	*Valvatae*	Australia, Qld, Heathlands	P.I. Forster 33759	BRI AQ0743438	KP867706	KP867699	KP867805	MN082934	–
Boronia stricta	*Boronia*	Australia, WA, Margaret River	M. Morley 319	PERTH 7799322	**OP654286**	**OP653875**	**OP654462**	**OP654385**	–
Boronia subulifolia	*Boronia*	Australia, NSW, Morton NP	M.F. Duretto 3116	NSW 1005447	**OP654287**	**OP653876**	**OP654463**	**OP654386**	–
Boronia ternata	*Valvatae*	Australia, WA, Boorabbin NP	M.J. Bayly 1931	MEL 2383603A	KP867726	KP867701	KP867777	MN082935	JN987080
Boronia ternata var. *elongata*	*Valvatae*	Australia, WA, Ravensthorpe Range	D.A. Young V#59	NSW 1006040	**OP654288**	**OP653877**	**OP654464**	**OP654387**	–
Boronia tetrandra	*Boronia*	Australia, cult. ANBG, ex Esperance, WA	J.W. Wrigley *s.n.*	CBG 36625.1	**OP654289**	**OP653878**	**OP654465**	**OP654388**	–
Boronia thujona	*Boronia*	Australia, NSW, Budderoo NP	M.J. Bayly 2007	MELU 105862	KP867717	KP867661	KP867802	MN082936	–
Boronia virgata	*Boronia*	Australia, WA (sensitive)	M. Sowry 96	PERTH 7690460	**OP654290**	**OP653879**	**OP654466**	**OP654389**	–
Boronia wilsonii	*Valvatae*	Australia, NT, Spirit Hills Conservation Reserve	D.L. Lewis 1713	NSW 924317	**OP654291**	**OP653880**	–	**OP654390**	–

Bold GenBank accession numbers are new sequences generated for this study. A dash (–) indicates missing data. Abbreviations are: ABGMA, The Australian Botanic Garden, Mount Annan; BMBG, The Blue Mountains Botanic Garden, Mount Tomah; NP, National Park; NSW, New South Wales; NT, Northern Territory; Qld, Queensland; RBGS, The Royal Botanic Garden, Sydney; SA, South Australia; SF, State Forest; Tas., Tasmania; Vic., Victoria; WA, Western Australia.

(the numbers in parentheses in the following paragraph indicate: the number of samples/the number of species sampled/the number of species currently placed in that section or placed *incertae sedis*), namely, *Alatae* (1/1/1); *Algidae* (5/3/3); *Boronella* (8/4/5; note: one sample not identified to species); *Boronia* (78/40/43); *Imbricatae* (1/1/1); *Pedunculatae* (11/5/11); *Valvatae* (22/20/66); and *incertae sedis* (10/4/4). Sampling included representatives of most of the five subsections and nine series of section *Valvatae*, the only section of *Boronia* to have a formal infrasectional classification. Species selected for the remaining sections were chosen to cover the morphological variation in those sections. We included 10 accessions of the 4 species placed *incertae sedis* in *Boronia*, *B. humifusa* (1), 2 subspecies of *B. inornata* (6), *B. ovata* (1) and *B. scabra* (2).

The outgroup comprised single accessions of seven species from the following six genera shown in previous studies to appropriately represent taxa closely related to *Boronia*: *Acronychia*, *Cyanothamnus*, *Euodia*, *Medicosma* Hook.f., *Phebalium*, and *Zieria*.

DNA extraction, PCR, sequencing, alignment

Leaf samples were taken from frozen silica-dried specimens or from herbarium sheets. The plant material was disrupted dry in a TissueLyser II (QIAGEN, Valencia, California, USA) by using tungsten beads, and total genomic DNA was extracted using the Qiagen DNeasy Plant Mini Kit, following the manufacturer's instructions. Five DNA regions were sequenced, namely, two nuclear regions, the external (*ETS*) and internal (*ITS*) transcribed spacers of the *18S–5.8S–26S* ribosomal DNA repeats; and three plastid regions, the *psb*A–*trn*H intergenic spacer (*psb*A–*trn*H), the *trn*L–*trn*F region (including the *trn*L intron and *trn*L–*trn*F intergenic spacer) and for a subset of 15 taxa, the *rbc*L gene. Sequence data for the *rbc*L gene were available for five outgroup taxa representing four genera, one or two taxa from five of the recognised sections in *Boronia*, and one taxon placed *incertae sedis*. We included the *rbc*L data, although missing from the majority of taxa, in the hope that it would test support for the major clades (see discussion on missing data and tree construction in Johnson *et al.* 2012). The following primers were used for PCR amplification and sequencing: *ETS*, *myrt*F (Lucas *et al.* 2007) and *ETS–18S* (Wright *et al.* 2001); *ITS*, *18SF* and *26SR* (Prince 2010) or *ITS5* and *ITS4* (White *et al.* 1990), with the former primer pair shown to be less likely to co-amplify fungal contaminants in extracts from herbarium material; *psb*A–*trn*H, *psbA*F (Sang *et al.* 1997) and *trnH*2 (Tate and Simpson 2003); *trn*L–*trn*F region, primers c and f (Taberlet *et al.* 1991); *rbc*L, RUT*rbc*L1F and *rbc*L1343R (Bayly *et al.* 2013).

All PCR reactions were performed in 25-µL volumes containing 200 µM of each primer, 200 µM of each dNTP, 0.004% bovine serum albumin, 2–2.5 mmol $MgCl_2$ and 1 U of *Taq* DNA polymerase. *ITS* and *trn*L–*trn*F amplifications used Promega GoTaq DNA polymerase (Promega Corporation, Madison, WI, USA), whereas amplifications for *ETS*, *rbc*L and *psb*A–*trn*H utilised Immolase DNA polymerase (Bioline, Luckenwalde, Germany) and a hot start PCR (with an initial cycle of 10 min at 95°C). PCR reactions were subjected to 40 cycles as follows: denaturation for 30 s at 94°C; annealing for 30 s at 50–58°C; and extension for 1 min at 72°C, with a final extension for 4 min at 72°C. The annealing temperature for *ETS*, *psb*A–*trn*H and *trn*L–*trn*F was 53°C, ITS (Prince) 58°C or (White) 55°C and *rbc*L 50°C. Double-stranded PCR templates were purified, and sequencing was performed by Macrogen Inc. (Seoul, South Korea).

Consensus sequences for each sample were assembled using ABI software Sequence Navigator (ver. 1.0.1, Applied Biosystems, Inc., Foster City, CA, USA) and aligned by eye in PAUP* (ver. 4.0a build 166, see http://phylosolutions.com/paup-test; Swofford 2003). In aligning sequences, gaps were positioned to maximise conformity to known indel types such as simple and inverted duplications of adjacent sequences (Levinson and Gutman 1987; Golenberg *et al.* 1993). Overlapping indels of different lengths, and insertions of the same length, but bearing different relationships to surrounding sequence, were treated as having independent origins, whereas indels of the same length and position and showing minor differences in nucleotide sequence were scored as the same state (Simmons and Ochoterena 2000). Potentially informative indels were scored as additional presence or absence characters and appended to the database. Gaps were treated as missing data in the phylogenetic analyses. Coding sequences of the *rbc*L gene were translated in MacClade (ver. 4.08a, see http://macclade.org/; Maddison and Maddison 2000) to check for internal stop codons. The full data matrix, including indel characters, is available in the 'Supplementary sequence' section in the Supplementary material. A 21-bp region containing a homoplastic inversion in *psb*A–*trn*H (highly incongruent with other characters) was excluded from all analyses.

Phylogenetic analyses

Separate analyses using maximum parsimony or Bayesian inference were run using either individual loci, the concatenated chloroplast or nuclear loci and the combined chloroplast and nuclear sequences. Heuristic searches of the combined or partitioned datasets were conducted in PAUP* (ver. 4.0a build 166, in the CIPRES Science Gateway, see https://www.phylo.org; Miller *et al.* 2010), by using tree bisection–reconnection branch-swapping to recover all equally most-parsimonious (MP) trees. One thousand replicates of random taxon-addition searching were conducted so as to detect multiple islands of trees, with subsequent use of the 'condense' option to delete duplicate trees. Multistate characters were treated as polymorphisms and swapping was performed on best trees. As searching exhausted computer memory for some partitions, restricted searching was employed, saving only 100 trees per replicate. Branch supports were calculated using jackknife (JK) rather than bootstrap resampling, following the recommendations of Simmons and Freudenstein (2011). Jackknife analyses utilised faststep searching in which each replicate was performed using random-sequence addition and no branch swapping, 10 000 replicates and the percentage of characters deleted in each replicate being set at one-third. Jackknifes were interpreted as >50–74% weak support for clades; >75–89% moderate support; 90–99% strong support; and 100% was considered robust.

The MP trees generated were compared with those obtained using the Markov-chain Monte Carlo (MCMC) method implemented in MrBayes (ver. 3.2.7a, see https://github.com/NBISweden/MrBayes/; Ronquist *et al.* 2012) in the CIPRES portal (Miller *et al.* 2010). Most appropriate nucleotide substitution models were determined using the Akaike's information criterion in MrModeltest (ver. 2.3, J. A. A. Nylander, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden, see https://github.com/nylander/MrModeltest2), with data being partitioned into the five regions indicated above and excluding the appended scored indels. All regions fit general time-reversible likelihood (GTR) substitution models (nst = 6), either with gamma distribution of rate variation among sites (GTR + Γ model; *trn*L–*trn*F), or also with a proportion of invariant sites (GTR + Γ + I model; *ETS*, *ITS*, *psb*A–*trn*H, *rbc*L).

Bayesian posterior probabilities (PP) were estimated using two independent runs of 10 million generations by using four chains, with tree sampling every 1000 generations. All parameters were set to be unlinked and with rates variable between partitions, with all other priors for the analysis being set flat (i.e. as Dirichlet priors). Runs were assessed as sufficient when checked for convergence with Tracer (ver. 1.7.1, see https://github.com/beast-dev/tracer/releases/tag/v1.7.1; Rambaut *et al.* 2018) and when the standard deviation of split frequencies approached 0.001. Trees generated prior to the four Markov chains reaching stationarity (burn-in ~25%) were discarded and the remaining trees were used to construct a 50% majority-rule consensus tree, with nodes assigned posterior probabilities (PP) of 0.95–1.00 considered supported. Clades with 100% JK and PP of 1.00 were considered fully supported. Bayesian analyses were conducted, including indels from all regions combined as an extra partition. For these analyses, the indels were binary encoded and we applied a default two-state Markov model with gamma distribution of rates and coding set to variable (as there were no invariant sites). State freqpr was set to fixed (empirical) to reflect having only two states. Inclusion of indels resulted in moderate improvements in branch supports, so final analyses included them as additional characters.

Morphology

Herbarium specimens held at the National Herbarium of New South Wales were examined for all species sampled in our molecular analyses to confirm morphological information in published descriptions as well as to identify additional morphological characters previously not documented.

Results

After exclusion of 38 bp of ambiguous sequence regions, the analysed 143 accessions, 85 species dataset comprised 5268 bp, including 1200 parsimony-informative (PI; 162 being scored indels) and 472 variable but parsimony-uninformative characters. The plastid portion comprised 3773 bp, of which 549 were informative, including 103 scored indels: *psb*A–*trn*H, 313 PI (75 included indels); *rbc*L, 36 PI (no indels); *trn*L–*trn*F, 200 PI (28 included indels). The nuclear portion comprised 1495 bp, of which 651 were informative, including 59 scored indels: *ETS*, 335 PI (including 30 indels); *ITS*, 316 PI (including 29 indels).

Separate analyses of the nuclear (Supplementary Fig. S1) or plastid (Supplementary Fig. S2) sequences retrieved the same major clades as did the combined analyses (Fig. 1, 2), and those clades here recognised as sections and series were also consistent throughout, excepting *Boronia* series *Persistens* Duretto & Heslewood (clade B1; formally described below), which was paraphyletic, but without jackknife support and with <0.95 posterior probability in the nuclear-only analysis. Although changes in structure were seen, the main differences were in support for clades and resolution of relationships within and between sections. In general, the jackknife supports for clades in the plastid-only analyses were weaker. On this basis our final analyses presented here focus on the combined molecular analyses, and we mention the separate analyses only where they highlight important differences. Likewise, parsimony and Bayesian analyses showed a high level of congruence, and Fig. 1 illustrates both jackknife (JK) clade support values >50% and posterior probabilities (PP) imposed on the major clades of the Bayesian majority-rule consensus tree.

The analysis of the combined dataset produced 100 000 equally most parsimonious trees of length of 4561 steps. Alignment of the nuclear loci was predominantly configured to deal with one or two base indels, whereas insertions in the plastid loci were predominantly longer repeats of adjacent sequence and at least one long deletion. A 21-bp inversion in *psb*A–*trn*H was homoplastic and that region was excluded from all analyses, with presence or absence of the inversion scored as an indel.

The genus *Boronia* was recovered with robust support (1.00 PP, 100% JK), and support for the four larger sections was either robust, as for *Boronia, Pedunculatae* and *Valvatae* (1.00 PP, 100% JK), or strong, as for *Boronella* (1.00 PP, 95% JK) (Fig. 1). The monotypic sections *Alatae* and *Imbricatae* are clearly highly divergent from other species. Section *Algidae* is polyphyletic in all analyses with the two

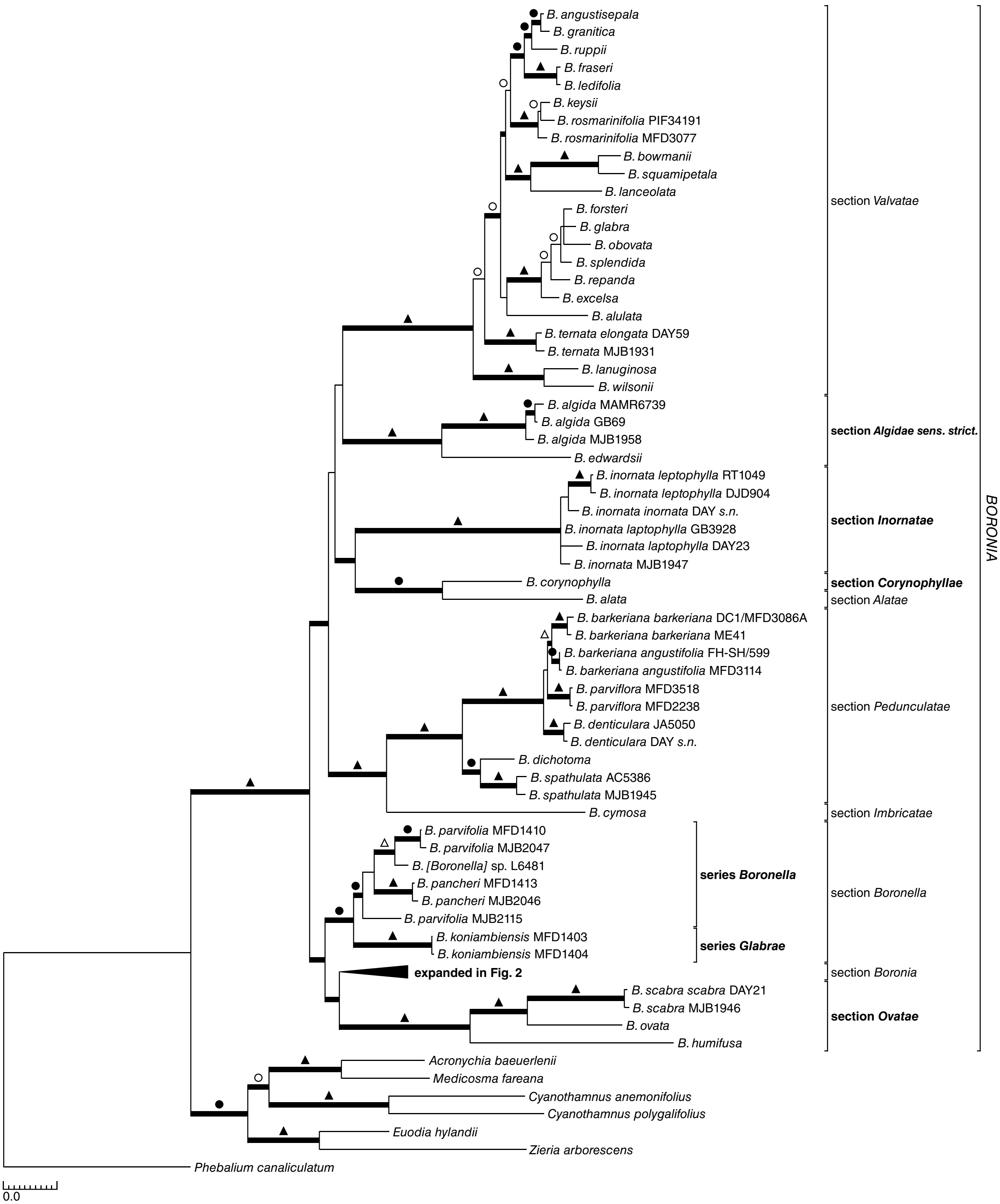

Fig. 1. Bayesian 50% majority-rule consensus tree from the combined analysis of two nuclear (*ITS*, *ETS*) and three plastid markers (*psb*A–*trn*H, *trn*L–*trn*F and *rbc*L), with thick lines showing supported clades (≥0.95 PP). Jackknife percentages from MP analysis are indicated with symbols above branches: 100% JK (closed triangle); 90–99% JK (closed circle); 75–89% JK (open triangle); 50–74% JK (open circle). New or revised sectional assignments are indicated in bold. Section *Boronia* clade has been collapsed and is shown in detail in Fig. 2.

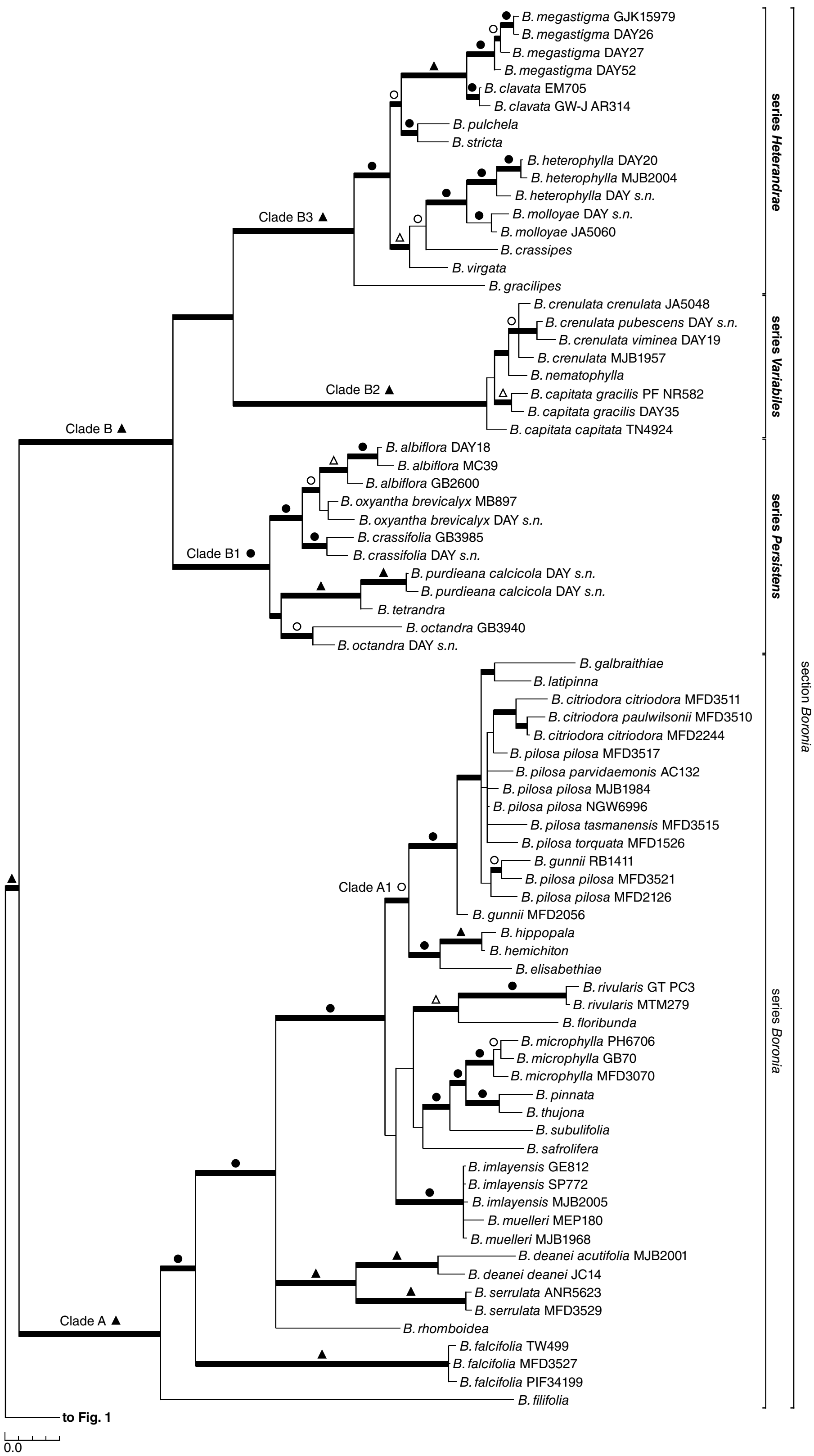

Fig. 2. Bayesian 50% majority-rule consensus tree from the combined analysis of two nuclear (*ITS*, *ETS*) and three plastid markers (*psb*A–*trn*H, *trn*L–*trn*F and *rbc*L) showing the expanded section *Boronia* clade from Fig. 1. Thick lines show supported clades (≥0.95 PP). Jackknife percentages from MP analysis are indicated with symbols above branches: 100% JK (closed triangle); 90–99% JK (closed circle); (75–89% JK (open triangl)e; 50–74% JK (open circle). New or revised series assignments are indicated in bold.

south-eastern Australian species, namely, *B. algida* F.Muell. and *B. edwardsii* Benth., forming a robust clade (1.00 PP, 100% JK; section *Algidae sens. strict.*) and the third species, *B. corynophylla*, always forming a south-western Australian clade with section *Alatae* that has strong support (1.00 PP, 98% JK).

Three of the four species currently placed *incertae sedis* in *Boronia* (Bayly *et al.* 2015; Duretto *et al.* 2020), namely, *B. humifusa*, *B. ovata* and *B. scabra*, form a robustly supported clade (1.00 PP, 100% JK). The fourth species, *B. inornata*, which is represented by six samples that form a robust clade (1.00 PP, 100% JK), is isolated, grouping with the section *Alatae* + *B. corynophylla* clade in the combined analysis (0.98 PP) and the analysis containing nuclear data only (1.00 PP). In the analysis using plastid data only, *B. inornata* is part of a weakly supported clade (54% JK) that also contains section *Valvatae*, section *Algidae sens. strict*., and the section *Alatae* + *B. corynophylla* clade.

The results confirmed that section *Boronella*, with *Boronia koniambiensis*, is monophyletic with strong support (1.00 PP, 95% JK). *Boronia koniambiensis* is sister to a clade containing multiple accessions of both *B. pancheri* (Baill.) Duretto & Bayly and *B. parvifolia* (Baker f.) Duretto & Bayly and an unidentified specimen in both the full analysis (1.00 PP, 92% JK) and the nuclear analysis. In the analysis of plastid sequences only, *B. koniambiensis* forms a trichotomy with one accession of *B. parvifolia* and a clade containing the remaining accessions.

Section *Boronia* contains two robustly supported clades, clade A (1.00 PP, 100% JK) containing all species found in south-eastern Australia (SE Austr.) and Tasmania (Tas.), and clade B (1.00 PP, 100% JK) containing all species from south-western Australia (Fig. 2). *Boronia citrata* N.G.Walsh (Victoria, Vic.), *B. coriacea* (SW Austr.) and *B. rozefeldsii* Duretto (Tas.) were the only species of section *Boronia* not included in the analysis because material was not available or could not be sequenced.

In clade A, *Boronia filifolia* F.Muell. (South Australia, SA; W Vic.) is sister to a strongly supported clade containing the remaining taxa in the combined analysis (1.00 PP, 90% JK) and the one using plastid data only. Resolution and support within the larger clade are generally poor, except for *B. falcifolia* A.Cunn. ex Endl. (SE Queensland, Qld; NE New South Wales, NSW) being sister to the remainder (1.00 PP, 96% JK) and two species relationships, *viz. B. imlayensis* Duretto with *B. muelleri* (Benth.) Cheel (multiple samples of each) forming a strongly supported polytomy (1.00 PP, 95% JK; SE NSW, E Vic.), and *B. deanei* Maiden & Benth. sister to *B. serrulata* Sm. (1.00 PP, 100% JK; both simple leaved, SE NSW). By contrast, much of the backbone of clade A is reduced to an unresolved polytomy in the nuclear-only analyses. A moderately supported clade A1 (1.00 PP, 93% JK), containing all species from Tasmania (except *B. rhomboidea* Hook., found in Tas. and SE NSW), western Victoria and South Australia (except *B. filifolia*) as well as *B. galbraithiae* Albr. from eastern Victoria, was recovered in the combined and nuclear-only analyses.

The south-western Australian clade B contains three strongly to robustly supported clades. Clade B1 (1.00 PP, 94% JK) contains *B. albiflora* R.Br. ex Benth., *B. oxyantha* Turcz., *B. crassifolia* Bartl., *B. octandra* Paul G.Wilson (one accession of this species groups with clade B3 in the nuclear analysis with poor support, that clade being sister to the remainder of B1), *B. purdieana* Diels, and *B. tetrandra* Labill. This clade is diverse morphologically but does have an identifiable morphological apomorphy, the petioles being persistent or tardily deciduous (staying on the stems after the lamina has fallen). Elsewhere in *Boronia*, they are deciduous with the leaves, or the leaves are sessile (M. F. Duretto, pers. obs.). Within this clade, a close relationship is supported between *B. tetrandra* and *B. purdieana* (1.00 PP, 100% JK) and among *B. albiflora*, *B. oxyantha* and *B. crassifolia* (1.00 PP, 99% JK).

Clade B2 (1.00 PP, 100% JK) contains *B. crenulata* Sm., *B. nematophylla* F.Muell. and a paraphyletic *B. capitata* Benth., which all have simple leaves (also found in clades A, B1, B2, and other sections) and woolly staminal filaments (also found in some species in section *Pedunculatae*) (Duretto *et al.* 2013). Clade B3 (1.00 PP, 100% JK) contains the remaining 10 species of clade B (*B. gracilipes* F.Muell. to *B. clavata* Paul G.Wilson) and is morphologically diverse and a morphological apomorphy was not identified for the group. Within clade B3, three strongly supported sister species pairs were identified, namely, *B. heterophylla* F.Muell. with *B. molloyae* J.Drumm. (1.00 PP, 98% JK), and *B. stricta* Bartl. with *B. pulchella* Turcz. (1.00 PP, 93% JK) in the combined and nuclear-only analyses, and *B. megastigma* Nees ex Bartl. with *B. clavata* Paul G.Wilson (1.00 PP, 98% JK).

Relationships between sections

The relationships among the sections and other major groups are poorly resolved, with conflict between analyses and little support for these larger clades. Relationships within sections or series also show conflict between analyses, with the nuclear dataset resolving more species as monophyletic. Of note is that section *Imbricatae* groups with section *Pedunculatae* (1.00 PP, 100% JK) and *B. corynophylla* groups with section *Alatae* in all analyses with strong support (see above). In the analyses using all data or only the plastid data there are two main clades, both with full support in the Bayesian analyses (1.00 PP), but no jackknife support; the first contains sections *Boronella* and *Boronia* with the *B. humifusa* + *B. ovata* + *B. scabra* clade, the last two clades being sister in the combined analysis. All other sections are in the second clade, which has poor internal support, apart from the section *Alatae* + *B. corynophylla* and section *Imbricatae* + section *Pedunculatae* clades. In the analysis using nuclear data, only section *Valvatae* is sister to a poorly supported clade (0.77 PP) containing all other groups and for which the internal structure is poorly supported, except for those outlined above.

Discussion

The genus *Boronia* and sections *Boronella*, *Boronia* (less *B. coriacea*), *Pedunculatae* and *Valvatae* are all monophyletic, confirming the results of Bayly *et al.* (2015) and Duretto *et al.* (2020). The two monotypic sections, *Alatae* and *Imbricatae*, are highly divergent from other taxa, supporting their status as sections, and suggestive of extended periods of isolation. Section *Algidae* is polyphyletic, with *B. corynophylla* grouping with section *Alatae* (discussed further below). The relationships of *B. humifusa*, *B. inornata*, *B. ovata*, *B. scabra* and *B.* ser. *Ovatae*, that were placed *incertae sedis* by Bayly *et al.* (2015), and the two morphologically distinctive species, *B. koniambiensis* and *B. corynophylla*, are resolved. *Boronia citrata*, *B. coriacea* and *B. rozefeldsii* were the only species of section *Boronia* not included in this molecular study, owing to suitable material not being available or could not be sequenced. The relationships of *B. citrata* and *B. rozefeldsii* are discussed below with section *Boronia* and that of *B. coriacea* with *B. inornata*.

The remainder of the discussion will focus on specific sections and sectional groups.

Placement of *Boronia humifusa*, *B. ovata*, *B. scabra* and *B.* series *Ovatae*

Boronia humifusa, *B. ovata* and *B. scabra* (all from SW Austr.) form a robustly supported clade that is clearly separated from section *Boronia*, confirming the conclusions of Bayly *et al.* (2015). Series *Ovatae* was described by Wilson (1971) under section *Imbricatae* to accommodate *B. ovata* and *B. scabra*, although later, when reviewing the genus, Wilson (1998) included the series as a synonym of a broadly defined series *Boronia*. *Boronia humifusa* was described by Wilson (1998) who noted the species was distinct in series *Boronia* (equivalent to the section *Boronia* of Bayly *et al.* 2015) in having petals with only one medial vein and lacking an apiculum on the abaxial surface, as well as a unique seed type. *Boronia humifusa*, *B. ovata* and *B. scabra* form a strongly supported clade with *B. humifusa*, sister to a clade containing the other two species, and all species are separated by long branches. This clade is possibly sister to a clade comprising section *Boronia* (Fig. 1), although this relationship is not supported in the separate analyses, and so warrants a similar rank. All three species have simple leaves, terminal inflorescences and seeds that are smooth or minutely tuberculate with a dorsal hilum that may or may not be in a shallow groove (Wilson 1971, 1998; Choi *et al.* 2012; Duretto *et al.* 2013). These three characteristics could be morphological synapomorphies for the group, although they are homoplasious characters in *Boronia*. Series *Ovatae* is raised to the rank of a section below (see Taxonomy).

Placement of *Boronia inornata* and *B. coriacea*

Boronia inornata is found in south-western Australia and one of its two subspecies is also found in South Australia. The species has large hemispherical glands on the branches (unusual but not unique in *Boronia*, see *B. algida* (section *Algidae*), *B. microphylla* Sieber ex Rchb. (section *Boronia*) and *B. bowmanii* F.Muell. (section *Valvatae*), for example), imparipinnate leaves with 3(5) usually terete leaflets, terminal inflorescences of 1(–3) flowers, and the seeds are microscopically tuberculate and do not have the sunken hilum that is typical of section *Boronia*. In all analyses, *B. inornata*, which is represented by numerous samples, forms a robustly supported clade (1.00 PP, 100 JK, Fig. 1) sister to the south-western Australian *B. alata* Sm. + *B. corynophylla* clade in the combined (PP 0.98) and nuclear Bayesian analyses.

Boronia coriacea is currently placed in section *Boronia* (Wilson 1971; Duretto *et al.* 2013; Bayly *et al.* 2015). Bayly *et al.* (2015) indicated that *B. coriacea* may be related to *B. inornata* and both species have glandular verrucose stems, leaves that are 3(5)-foliolate, terminal inflorescences with few flowers, imbricate sepals and petals, petals with an obscure apiculum on the abaxial surface, and glabrous stamens. The two species differ in that *B. inornata* has leaflets that are usually terete and flowers that are usually solitary on short pedicels, whereas *B. coriacea* has flat leaflets, and an inflorescence of a few flowers that are on longer pedicels. The seed morphology of *B. coriacea* has not been documented, and Wilson (1971), who described the species, and Duretto *et al.* (2013), in the *Flora of Australia*, do not discuss its relationships. The features these two species share are not unique in *Boronia*, but the combination is. Apart from the aestivation of the petals the species are similar to *B. algida* (section *Algidae*) in appearance. *Boronia inornata* does not group with any species of section *Algidae* in our analyses.

Boronia inornata is isolated from all other species in this analysis and a new section, section *Inornatae* Duretto & Heslewood, is formally described below to accommodate it. As *B. coriacea* is morphologically similar to *B. inornata*, it is also placed in this newly described section.

Sections *Algidae* and *Alatae* and the placement of *Boronia corynophylla*

Boronia section *Algidae* is polyphyletic with its three species never grouping together. The south-eastern Australian clade containing *B. algida* (NSW, ACT, Vic.), the type species of the section, and *B. edwardsii* (SA) has strong support and is isolated with no clear affinity, with only the nuclear Bayesian analysis resolving it as sister to section *Ovatae* (0.99 PP, Supplementary Fig. S1). A narrower circumscription of the section, section *Algidae sens. strict.* (Fig. 1, S1, S2), is provided below in Taxonomy and the section can be defined by having imparipinnate leaves with flat leaflets, terminal inflorescences of 1(–3) flowers, imbricate sepals, valvate petals and globose stigmas that are much wider than the style.

Boronia corynophylla is restricted to a small area in inland south-western Australia and shows a strongly supported relationship with *B. alata*. *Boronia alata* is the sole member of section *Alatae* and is widespread in near coastal areas of south-western Australia. Branch lengths to both species are long, suggesting that they have had an extended period of isolation. This pairing is surprising, given the striking morphological differences between the two species, although they both have valvate petals. *Boronia corynophylla* has an exfoliating cuticle on its branches, which gives the branches a glaucous appearance and is unique in *Boronia*, in addition to simple, slender, terete leaves and an inflorescence of 1(–3) flowers and valvate petals. By contrast, *B. alata* has smooth branches, imparipinnate or bipinnate leaves with broad leaflets, inflorescences that are large, cymose panicles, and valvate and reduplicate petals. Seeds, which provide useful characters at the section and series level in *Boronia* (Wilson 1998; Choi *et al.* 2012), have not been documented for *B. corynophylla*. With regard to a formal taxonomy, one alternative would be to expand section *Alatae* to accommodate *B. corynophylla* but this would create a heterogenous assemblage with no clear apomorphies. Therefore, as *B. corynophylla* is clearly isolated taxonomically, a new monotypic section, *Corynophyllae* Duretto & Heslewood, is formally described below to accommodate it. This will be the fourth section of *Boronia*, three of which are monotypic, that is endemic to south-western Australia.

Section *Boronella*

Boronia section *Boronella* contains four described species, the three sampled here plus *B. hartleyi* Duretto & Bayly (Hartley 1995; Morat *et al.* 2011; Bayly *et al.* 2015; T. G. Hartley, unpubl. data) and an undescribed species (T. G. Hartley, unpubl. data; M. F. Duretto, pers. obs.; called *B.* sp. S'ern Grande Terre (McPherson 3961) at the National Herbarium of NSW). *Boronia koniambiensis* is sister to the remaining species in all but the analysis using only plastid data where one accession of *B. parvifolia* forms a trichotomy with *B. koniambiensis* and a clade containing the remaining specimens. *Boronia hartleyi* and *B.* sp. S'ern Grande Terre (McPherson 3961) are similar morphologically to *B. pancheri* and *B. parvifolia* (T. G. Hartley, unpubl. data; M. F. Duretto, pers. obs.). These four species all have verticillate leaves, branches with tufts of simple hairs in the axils of the leaves and at the base of the pedicels, inflorescences that are terminal pseudo-umbels, and narrowly imbricate petals (Hartley 1995; Bayly *et al.* 2015; T. G. Hartley, unpubl. data; M. F. Duretto, pers. obs.). By contrast, *B. koniambiensis* has opposite decussate leaves, glabrous branches, inflorescences that are terminal cymes, and petals that are valvate in bud (Hartley 1995; Bayly *et al.* 2015; T. G. Hartley, unpubl. data; M. F. Duretto, pers. obs.). Valvate petals have arisen several times in *Boronia* (see discussion above; Duretto and Ladiges 1998; Bayly *et al.* 2015) but in the *Boronia* + *Boronella* + *Ovatae* clade of the combined and plastid only analyses, they are unique to *B. koniambiensis* and, so, could be considered an apomorphy for that species. In no analysis was a clade retrieved of only those taxa with valvate petals. The remaining species of section *Boronella* are united on the basis of their verticillate leaves (not found elsewhere in *Boronia*, except very rarely in individual plants of a very few species, e.g. *B. rosmarinifolia* A.Cunn. ex Endl. (section *Valvatae*)), pseudo-umbellate inflorescences (seen also in sections *Pedunculatae* and *Valvatae*) and the tuft of simple hairs in the axils of the leaves and at the bases of the pedicels.

Section *Boronella* has a number of morphological apomorphies such as branchlets with the cortex articulated at nodes, cotyledons that are wider than the hypocotyl, and the presence of a hypodermis in the leaves (Foster 1955; Weston *et al.* 1984; Hartley 1995; Kubitzki *et al.* 2011; Bayly *et al.* 2015). There are two clearly defined clades in section *Boronella* and both are well supported by both morphological and molecular data and so warrant taxonomic recognition. Hartley (1995) did note that *Boronia koniambiensis*, when transferring this species from *Boronia* to the genus *Boronella*, was different from the remainder of the species in *Boronella*, but concluded that *Boronella* should be retained as one genus and that a new monotypic genus should not be erected for *B. koniambiensis*. We follow Hartley's argument here, at the sectional level, and retain the one section for all New Caledonian species of *Boronia* but classify them into two series, namely, a new monotypic series for *B. koniambiensis*, series *Glabrae* Duretto & Heslewood, which is formally described below, as well as the typical series for the remaining species (see Taxonomy).

Section *Boronia*

The circumscription of *Boronia* section *Boronia* (only *B. citrata* and *B. rozefeldsii* not sampled for this molecular study) is similar to that outlined by Bayly *et al.* (2015), apart from the removal of *B. coriacea* (now placed in section *Inornatae*), which they had provisionally placed in section *Boronia*. Both unsampled species can be placed in section *Boronia* on the basis of morphology (see Albrecht and Walsh 1993; Duretto 2003). The section has a unique seed type: the testa is smooth and the adaxial hilum is linear and sunken in a groove that is surrounded by glossy labiose margins (Wilson 1998; Choi *et al.* 2012). Within the section, there are two well-supported clades, namely, clade A containing species found in south-eastern Australia and Tasmania (*B. citrata* and *B. rozefeldsii* not sampled) and including the type species of *Boronia*, *B. pinnata* Sm., and clade B with all south-western Australian species. There are no obvious morphological characters, or combinations of characters, supporting either of these clades. However, most species in clade A have pedunculate, open and multi-flowered inflorescences (exceptions are the simple leaved *B. deanei*, *B. rhomboidea*, *B. serrulata* and some Tasmanian species), whereas those in clade B usually have flowers that are solitary or paired, although small cymes are also present in all species of clade B2, and three-flowered cymes are also present in *B. stricta* and *B. virgata* Paul G.Wilson of clade B3.

The internal structure within clade A is not well supported and there is significant conflict between analyses. In the combined and plastid analyses, *B. filifolia* (SA, W Vic.) is resolved as sister to a clade containing the remainder of the species. This species is unusual in the section in being glabrous apart from the flowers and having filiform leaves or leaflets. Very narrow leaves are also found in *B. deanei* (NSW), which is also glabrous apart from a raised ring of tuberculae on the glands on the stems and leaves. Structure within the remainder of clade A is not well supported, although *B. falcifolia* (coastal NSW, SE Qld) is sometimes sister to a clade of the remaining species. In the combined (1.00 PP, 58 JK) and nuclear (1.00 PP) analyses, there is also a large polytomy (clade A1) with all Tasmanian species (excepting *B. rhomboidea*) as well as most species found in western Victoria and South Australia (apart from *B. filifolia*).

The south-western Australian clade (clade B), in contrast to the south-eastern Australian clade, has well-supported structure and contains three strongly to robustly supported clades (clades B1, B2, B3). Clade B1 is characterised by persistent or tardily caducous petioles (falling after the lamina has fallen) and the species within it show considerable morphological variation. Clade B2 is characterised by woolly staminal filaments (unique in section *Boronia*) and simple leaves (widespread in *Boronia*). The names *Boronia* series *Variabiles* Benth. (type: *B. crenulata*) and series *Terminales* Benth. (type: *B. capitata*) are both available for clade B2 and were published in the same publication, and the former is chosen here. Clade B3, as with clade B1, contains significant morphological variation, and like clades A and B, lacks clearly discernible morphological apomorphies. The name *Boronia* series *Heterandrae* Benth. (type: *B. megastigma*) is available for this clade.

Most species of *Boronia* have simple flowers without much modification, typical of most members of the family Rutaceae, that is, a fully open, pink or white corolla, erect stamens that are longer than the ovary, anthers that are approximately equal in size and fertile, and a cylindrical style topped with a minute stigma. Within both clades B1 and B3, there are suites of species with highly modified flowers that appear to be driven by specialised pollinator associations with day moths of the family Heliozelidae (Milla 2019; Wild 2022; L. Milla *et al*., in prep.). Clades B1 and B3 resolve together in the nuclear-only analyses, hinting at a possible shared origin of some of these features. For example, sterile antesepalous anthers that are significantly different in size from the antepetalous anthers occur in both clades B1 and B3. In clade B1, *B. purdieana* and *B. tetrandra* are sister species that have minute sterile antisepalous anthers. By contrast, in clade B3, *B. megastigma* (sister species of *B. clavata*), and the sister taxa *B. heterophylla* and *B. molloyae*, have very large, dark-coloured, sterile, antesepalous anthers. All these species, with *B. clavata*, have very large stigmas and, in both clades, some species have stigmas that have antesepalous lobes: in B1, *B. purdieana* and *B. tetrandra*, and in B3, *B. megastigma* (see Duretto *et al.* 2013, fig. 24). There are several other floral features that appear to be associated with specialised pollinator–host associations, including pendulous flowers, cup-shaped flowers, unusual petal colours (e.g. green, yellow, red, brown), contrasting petal colours (*B. megastigma* where the adaxial surface is yellow and abaxial surface is brown), variously shaped stamens, lobed or hairy discs, sunken ovaries, absent styles and large stigmas (see descriptions in Duretto *et al.* 2013). There is a diversity of floral forms that interestingly does not lend itself to a formal classification as there are many other species with more typical flowers related to these clades. Most species in south-eastern Australia and Tasmania have simple unmodified flowers. However, two species of clade A, namely, *B. serrulata* and *B. floribunda* Sieb. ex Rchb. (both confined to the Sydney region sandstones, NSW), also have modified flowers with large spherical stigmas and filaments with a dense tuft of hairs at the apex. Curiously these species are not sister taxa and the features seem to be a case of parallel evolution. This association and apparent co-evolution of certain moths of the family Heliozelidae with their host species are part of another study (Milla 2019; L. Milla *et al*., in prep.) and will not be dealt with further here.

A taxonomic challenge in *Boronia* section *Boronia* is that there are several clades that are strongly supported by both molecular and morphological data, including B1 (persistent or tardily caducous petioles), B2 (woolly filaments) and the species pairs in clades B1 and B3 discussed above. By contrast, clades A, B and B3 have good to strong support in the analyses presented here but do not have readily identified morphological apomorphies. This is similar to the situation seen in other Australian genera in Rutaceae, for example, *Asterolasia* F.Muell. and *Phebalium* Vent., where there is strong molecular support for clades that are confined to either eastern or south-western Australia, but no obvious morphological characters to support the clades (Duretto *et al.* 2023). One of the roles of a cladistic analysis is to identify well-supported groups that then can be recognised in a preferably robust formal taxonomy, which is very useful in larger taxonomic groups such as *Boronia*. Robust formal classification helps with the development of identification tools, identification of conservation priorities, as well as the placement of taxa new to science, which is continuing in *Boronia* (e.g. Barrett *et al.* 2015; Duretto 2019).

There are a number of options available on how to proceed with the classification of the species in section *Boronia*. One would be to retain the current classification with no further grouping of the species. A second would be to formally recognise those clades with morphological synapomorphies as series (clades B1, B2, *B. megastigma* + *B. clavata* etc.) and leave the remainder as *incertae sedis*. Unfortunately, the type species, *B. pinnata*, is one of the many species not part of a morphologically well-defined group. A third option is to formally recognise the four major clades with strong to robust molecular support (clades A, B1, B2, B3) as series, acknowledging that two of these are difficult to identify on morphological grounds but that all have support on the basis of molecular data. Option three does not create significant issues nomenclaturally: clade A retains the name *Boronia* as it contains the type species; clade B1 does not have an available name but is easily defined and thus can be formally described; clade B2 has two available names at the appropriate rank (of equal priority as they are described in the same publication and have never been considered synonymous) and is easily defined on morphological grounds; and clade B3 has a name available at the appropriate rank. The issue here is that both clades A and B3 do not have morphological apomorphies and are diverse morphologically. The result would be a complicated key to series, which is not an insurmountable issue, just not ideal. We are applying the third option (see Taxonomy).

Boronia sections *Imbricatae* and *Pedunculatae*

Boronia sections *Imbricatae* (1 sp., *B. cymosa* Endl., SW Austr.) and *Pedunculatae* (11 spp.; SW Austr., SE Austr., Tas.) have a well-supported relationship in all analyses (Fig. 1, S1, S2) supporting the results found in Bayly *et al.* (2015). This close relationship between *B. cymosa* and the species placed in section *Pedunculatae* has been postulated before. Both Bentham (1863) and Engler (1896, 1931) placed *B. cymosa*, along with species from other sections, with several Western Australian species of section *Pedunculatae* in series *Pedunculatae* Benth., although they both placed the known eastern Australian species of section *Pedunculatae, B. parviflora* Sm., in series *Terminales* Benth. Engler (1896, 1931) placed both these series, and four others, in a broadly defined section *Imbricatae*. Wilson (1971) circumscribed section *Imbricatae* to include only three series, series *Imbricatae* (Engl.) Paul G.Wilson (with only *B. cymosa*), series *Pedunculatae* (SW Austr. species only; he did not discuss *B. parviflora* or *B. barkeriana* F.Muell.) and series *Ovatae* (*B. scabra* and *B. ovata*). Wilson (1971) did not discuss the rationale behind this novel classification.

Species of section *Imbricatae* and section *Pedunculatae* have simple leaves and terminal inflorescences, both widespread characters in *Boronia*, but differ significantly in flower and seed morphology (Wilson 1971, 1998; Choi *et al.* 2012; Duretto *et al.* 2013). Section *Imbricatae* is characterised by imbricate and persistent sepals, and glaucous, rugulose seeds with a dorsal aril, whereas section *Pedunculatae* is characterised by valvate and usually deciduous sepals, and smooth, shiny seeds with a basal raphe that is a pulpy mass at the base of the seed (Wilson 1998; Duretto *et al.* 2013). As the sections are both well supported by both morphological characters and the molecular data presented here, we retain each section as distinct.

Boronia section *Valvatae*

Boronia section *Valvatae* is well supported by both morphological (Duretto and Ladiges 1998; Duretto 1999) and molecular data (see above; Bayly *et al.* 2015; Duretto *et al.* 2020). Morphological apomorphies that support the section are the presence of stellate hairs (unique in *Boronia*), valvate sepals (also found in section *Pedunculatae*), and valvate petals (also found in sections *Algidae, Alatae, Corynophyllae* and *Boronella* (series *Glabrae*)) and persistent petals (also found elsewhere in *Boronia*). The internal structure of the section does not agree with the classification of the section on the basis of morphological data (Duretto and Ladiges 1998; Duretto 1999, 2008; Duretto *et al.* 2013), but because only 20 species of the 66 species were sampled, it would be premature to propose any changes to the current classification.

Relationships between the sections of *Boronia* and phylogenetic diversity

The resolution of relationships between the 10 sections of *Boronia* is not conclusive, apart from the close relationship of section *Alatae* with section *Corynophyllae*, and that of section *Imbricatae* with section *Pedunculatae* in all analyses (Fig. 1, S1, S2). In the combined maximum-parsimony analysis, these two clades formed a polytomy with the remaining six sections. The Bayesian analysis contained more structure with sections resolving into two well-supported clades. The first contains sections *Boronia* and *Ovatae* sister with robust support (1.00 PP) and these sister to *Boronella* (1.00 PP). The second clade contains the remaining seven sections with little internal support except for the strongly supported *Imbricatae* + *Pedunculatae* and *Alatae* + *Corynophyllae* clades and the latter sister to section *Inornatae* with good support (0.98 PP).

Of the 10 sections recognised here, 6 contain 3 or fewer species. The three monotypic sections, *Alatae*, *Corynophyllae* and *Imbricatae*, along with section *Ovatae* (3 spp.), are confined to south-western Australia. Two sections contain two species, namely, *Algidae sens. strict.* from south-eastern Australia, and *Inornatae* from south-western Australia and South Australia. Sections *Boronia* (43 spp.) and *Pedunculatae* (11 spp.) are both found in south-eastern Australia (including Tas.) and south-western Australia. The largest section, *Valvatae* (66 spp.), is found in south-western Australia, eastern Australia (being absent from SA and Tas.) and north-western Australia, and is the only section found in tropical

Australia. The final section, *Boronella* (4 or 5 spp.), is confined to New Caledonia.

South-western Australia contains significant phylogenetic diversity with 8 of the 10 sections present, 4 of which are endemic to the region. The two Australian sections with infrasectional classifications demonstrate contrasting patterns, with the phylogenetic diversity of section *Boronia* being higher in south-western Australia, whereas that for section *Valvatae* is higher in eastern and northern Australia.

Taxonomy

Boronia Sm., *Tracts Nat. Hist.* 288 (1798)

Type: *Boronia pinnata* Sm.

Perennial herbs, shrubs, rarely small trees; glabrous or with simple or stellate hairs. Leaves opposite, decussate, rarely in whorls of three (see series *Boronella*), simple or imparipinnate or rarely bipinnate (see section *Alatae*). Inflorescences axillary or terminal; flowers solitary or in cymes or pseudo-umbels or panicles, bisexual, 4-merous, rarely 5-merous (*B. scabra* subsp. *attenuata* Paul G.Wilson). Sepals free, open, imbricate or valvate, persistent or caducous. Petals free, imbricate or valvate, not obviously glandular; tip straight or with a subterminal apiculum on the abaxial surface; 1- or 3-veined at base; caducous or persistent. Stamens 8, rarely 4 of them caducous (*B. parviflora*); filaments usually inwardly curved, semiterete, glabrous or hairy, usually verrucose towards apex; anthers introrse, apiculate or not, connective usually inconspicuous or cream coloured, all or only antepetalous anthers fertile (see series *Boronia* and series *Persistens*). Disc prominent, usually entire, rarely with antepetalous (*B. octandra*) or antesepalous (*B. tetrandra*) lobes. Carpels 4; ovaries free though united at apex on adaxial margin by the solitary style. Fruit of 1–4 basally connate follicles (cocci), dehiscing explosively ventrally with separating, elastic endocarp. Seed: sclerotesta smooth or minutely tuberculate, rarely prominently rugulose (*B. cymosa*), glossy or dull. (Adapted from Duretto *et al.* 2020).

An Australian (including Tasmania) and New Caledonian genus of 134 species classified into 10 sections, including 9 confined to Australia, and 1, section *Boronella*, to Grande Terre, New Caledonia. Two sections, *Corynophyllae* and *Inornatae*, are newly described, and a new combination at sectional level is made for section *Ovatae*. Novel infrasectional classifications are provided for sections *Boronella*, with two series, and *Boronia*, with four series. Sections *Alatae*, *Imbricatae*, *Pedunculatae*, apart from the addition of subspecies for *B. denticulata* Sm. (Duretto 2019), and *Valvatae*, apart from the addition of five species (Barrett *et al.* 2015), remain as previously circumscribed by Duretto *et al.* (2013) and Bayly *et al.* (2015) and are not dealt with further here.

Key to the sections of *Boronia*

1. Branches, including cortex, strongly articulated at nodes; leaves verticillate in whorls of three, or opposite–decussate; cotyledons elliptic or suborbicular, wider than hypocotyl (New Caledonia)..section ***Boronella***
Branches, including cortex, continuous (smooth) at nodes; leaves opposite–decussate; cotyledons linear, as wide as hypocotyl (Austr., Tas.)...2
2. Petal aestivation known...3
Petal aestivation unknown..13
3. Petals valvate in bud..4
Petals imbricate in bud...7
4. Inflorescence axillary; stellate hairs present (sometimes only on flowers), rarely absent (Kimberley Region, WA), simple hairs also present (tropical, eastern and southern Austr.)................... ....section ***Valvatae***
Inflorescence terminal; all hairs simple (Southern Austr., Tas.)......5
5. Leaves simple..section ***Corynophyllae***
Leaves imparipinnate..6
6. Inflorescence a many-flowered cymose panicle; peduncle present; leaves imparipinnate or bipinnate (SW Austr.)......section ***Alatae***
Inflorescence cymose, 1(–3)-flowered; peduncle absent; leave imparipinnate (SE Austr.).................................section ***Algidae***
7. Leaves imparipinnate..8
Leaves simple..9
8. Inflorescence axillary, sometimes also terminal, 1–40 + -flowered; stems smooth or glandular verrucose; staminal filaments glabrous or hairy..section ***Boronia***
Inflorescence terminal, sometimes also terminal on short axillary branches, 1–3-flowered; stems glandular verrucose; staminal filaments glabrous...section ***Inornatae***
9. Seed rugulose; branches glabrous, developing a visible cream-coloured spongy layer with age....................section ***Imbricatae***
Seed smooth though sometimes minutely tuberculate; branches glabrous or hairy, not developing a visible cream-coloured spongy layer...10
10. Seeds with a cream-coloured pulpy elaiosome at base; sepals valvate and usually caducous; branches glabrous or rarely woolly; inflorescence terminal, sometimes also upper axillary................ ....section ***Pedunculatae***
Seeds without a basal elaiosome; sepals imbricate, persistent; branches glabrous or hairy; inflorescence terminal or axillary......11
11. Staminal filaments woolly–ciliate.. ....(section *Boronia*) series ***Variabiles***
Staminal filaments pilose, puberulous or glabrous.....................12
12. Inflorescence axillary, 1–5-flowered, rarely in terminal cymes and then leaves broadly obovate to almost circular......................... ....section ***Boronia***
Inflorescence in terminal and upper-axillary cymes, few to many-flowered; leaves narrowly oblong to oblong–elliptic or broadly ovate...section ***Ovatae***
13. Stellate hairs present (sometimes only on flowers), simple hairs also present; inflorescence axillary (N and SW WA, NT, Qld, NSW, Vic.)..section ***Valvatae***
All hairs simple; inflorescence axillary or terminal (N and SW WA, Qld, NSW, Vic., Tas., SA)...14
14. Leaves imparipinnate...15
Leaves simple...19
15. Inflorescence axillary, sometimes also terminal.........................16
Inflorescence terminal, sometimes also terminal on short axillary branches...17
16. Antepetalous anthers smaller than or equal to antesepalous anthers, if larger then branches hairy (southern Austr.)........................... ....section ***Boronia***

Antepetalous anthers much larger than antesepalous anthers; branches glabrous (Kimberley Region, N WA)............................ ....(section ***Valvatae***) subsection ***Anomalae***

17. Inflorescence a many-flowered cymose panicle; staminal filaments pilose; leaves imparipinnate or bipinnate............section ***Alatae***
Inflorescence cymose, 1–5-flowered; staminal filaments glabrous; leaves imparipinnate...18

18. Stigma globular, much wider than style; leaves 3–9-foliolate; seed dull...section ***Algidae***
Stigma minute, as wide as style; leaves 3(5)-foliolate; seed shiny...section ***Inornatae***

19. Seed rugulose; branches glabrous, developing a visible cream-coloured spongy layer..................................section ***Imbricatae***
Seed smooth though sometimes minutely tuberculate; branches glabrous or hairy, not developing a visible cream-coloured spongy layer...20

20. Seeds with a cream-coloured pulpy elaiosome at base; sepals valvate, usually caducous; branches glabrous or rarely woolly; inflorescence terminal, sometimes also upper axillary.......section ***Pedunculatae***
Seeds without a basal elaiosome; sepals imbricate, persistent; branches puberulous, pilose or glabrous; inflorescence terminal or axillary..21

21. Leaves terete; inflorescence terminal; branches exfoliating and with a grey scurfy covering............................section ***Corynophyllae***
Leaves flat or terete, if terete then flowers axillary; branches various but not exfoliating or having a grey scurfy covering...............22

22. Staminal filaments woolly–ciliate.. ....[section ***Boronia***] series ***Variabiles***
Staminal filaments puberulous, pilose or glabrous.....................23

23. Inflorescence axillary, 1–5-flowered, rarely in terminal cymes and then leaves broadly obovate to almost circular......section ***Boronia***
Inflorescence in terminal and upper-axillary cymes, few–many-flowered; leaves narrowly oblong to oblong–elliptic or broadly ovate..section ***Ovatae***

Boronia section ***Algidae*** Duretto, *Muelleria* 12: 16 (1999)

Type: *Boronia algida* F.Muell.

Hairs simple. Branches, including cortex, not articulated (continuous) at nodes, puberulous, smooth or glandular verrucose. Leaves opposite–decussate, imparipinnate. Inflorescence terminal, cymose, 1–3-flowered; peduncle absent; bracts and bracteoles persistent. Sepals imbricate in bud, persistent. Petals valvate in bud, without a subterminal apiculum on abaxial surface, multiveined from base, persistent or caducous. Staminal filaments glabrous, swollen and verrucose towards apex, with tip appearing subterminal adaxially. Stigma globular, much wider than style. Seed dull, grey to black; adaxial surface with a linear hilum; raphe basal; sclerotesta sometimes minutely verrucose; cotyledons linear, as wide as hypocotyl.

A section of two species confined to south-eastern Australia: *Boronia algida* (NSW, ACT, Vic.), *B. edwardsii* (SA).

Boronia section ***Boronella*** (Baill.) Duretto & Bayly, *Austral. Syst. Bot.* 28: 119 (2015)

Boronella Baill., *Adansonia* 10: 302 (1872). *Type*: *Boronella pancheri* Baill. [≡*Boronia pancheri* (Baill.) Duretto & Bayly].

Hairs simple. Branches, including cortex, strongly articulated at nodes, glabrous or with hairs at nodes, smooth or cuticle slightly exfoliating, not obviously glandular. Leaves verticillate in whorls of three or opposite–decussate, simple. Inflorescence a terminal cyme or pseudo-umbel, many-flowered; peduncle absent or present; bracts and bracteoles deciduous or apparently absent or so minute they are obscured by hairs at base of pedicels. Sepals imbricate or valvate in bud, persistent. Petals imbricate or valvate in bud, usually with a subterminal apiculum on abaxial surface, mostly multiveined from base or with steeply ascending basal lateral veins, persistent. Staminal filaments glabrous or hairy, swollen and verrucose towards apex, tip usually appearing subterminal adaxially. Stigma minute, not or slightly wider than style. Seed shiny, with a smooth sclerotesta, although cell walls visible; hilum usually adaxial and linear; raphe small and covered by brown outer testa; cotyledons elliptic or suborbicular, wider than hypocotyl.

A section of at least five species, of which four have been formally described, that is confined to Grande Terre, New Caledonia. A key to the described species of the genus *Boronella* has been provided by Hartley (1995). Here we present the first infrageneric classification for section *Boronella,* which includes two series.

Key to the series of *Boronia* section *Boronella*

1. Leaves verticillate in whorls of 3, sometimes also opposite–decussate on the same plant; branches glabrous apart from a dense indumentum in leaf axils and at base of inflorescence; petals imbricate in bud...series ***Boronella***
Leaves opposite–decussate; branches glabrous; petals valvate in bud...series ***Glabrae***

Boronia [section ***Boronella***] series ***Boronella*** (Baill.) Duretto & Heslewood, comb. nov.

Boronella Baill., *Adansonia* 10: 302 (1872). *Type*: *Boronella pancheri* Baill. [≡*Boronia pancheri* (Baill.) Duretto & Bayly].

Branches glabrous apart from a dense indumentum of simple hairs in leaf axils and at base of inflorescence. Leaves verticillate in whorls of 3, sometimes also opposite–decussate on some plants. Inflorescence a simple terminal cluster (pseudo-umbel), bracts and bracteoles absent or possibly minute and obscured by hairs at base of pedicels. Petals imbricate in bud.

A series of at least four species confined to Grande Terre, New Caledonia: *Boronia hartleyi, B. pancheri, B. parvifolia, B.* sp. S'ern Grande Terre (McPherson 3961) (phrase name used at the National Herbarium of NSW; T. G. Hartley, unpubl. data; M. F. Duretto, pers. obs.).

Boronia [section *Boronella*] series *Glabrae* Duretto & Heslewood, ser. nov.

Type: *Boronia koniambiensis* Däniker.

Differs from series *Boronella* by the glabrous branches (*v*. pilose at nodes), opposite–decussate leave (*v*. verticillate in whorls of 3), and petals being valvate in bud (*v*. imbricate in bud).

Branches glabrous. Leaves opposite–decussate. Inflorescence a terminal cyme; bracts and bracteoles deciduous. Petals valvate in bud.

A monotypic series confined to the Koniambo Massif, north-eastern Grande Terre, New Caledonia.

Etymology

The series epithet is derived from the Latin *glabrus* alluding to the glabrous branches, which is one of the features that distinguishes this species from all other species in section *Boronella*.

Boronia Sm. section *Boronia*

Type: *Boronia pinnata* Sm.

Hairs simple. Branchlets, including cortex, not articulated (continuous) at nodes, smooth or glandular–verrucose, glabrous or hairy. Leaves opposite–decussate, simple or imparipinnate. Inflorescence axillary or terminal, flowers solitary or in cymes, 1–40+-flowered; peduncle absent or present; bracts and bracteoles persistent. Sepals open or imbricate in bud, persistent. Petals imbricate in bud, with subterminal apiculum on the abaxial surface, multiveined from base or with steeply ascending basal lateral veins. Staminal filaments glabrous or hairy, swollen and usually verrucose, rarely smooth, towards apex, with tip usually appearing subterminal adaxially. Stigma minute and scarcely wider than style or massive. Seed with a smooth sclerotesta, cell walls not usually visible, glossy; hilum adaxial, linear, usually in a groove with labiose margins; raphe small and covered by brown outer testa; cotyledons linear, as wide as hypocotyl.

A section of 43 species found across southern Australia, including Tasmania, with 24 species confined to south-eastern Australia and 19 to south-western Australia. The section outlined here is equivalent to that described as section *Boronia* by Bayly *et al.* (2015) less *B. coriacea*, and *Boronia* ser. *Boronia* by Duretto *et al.* (2013), less *B. coriacea*, *B. inornata*, *B. humifusa*, *B. ovata* and *B. scabra*. A key to the species is provided by Duretto *et al.* (2013). No novel species for the section have been formally described since Duretto *et al.* (2013) though *B. clavata* has recently had novel subspecies formally described (Duretto 2019).

Here we present a novel infrageneric classification of the section that includes four series, including one newly described and two reinstated.

Key to the series of *Boronia* section *Boronia*

1. Staminal filaments woolly; leaves simple..............series ***Variabiles***
Staminal filaments pilose, puberulous or glabrous; leaves simple or imparipinnate...2
2. Petioles persistent or tardily caducous and after lamina has fallen; leaves imparipinnate; anthers approximately equal or antisepalous anthers much smaller than antipetalous anthers.......................... ....series ***Persistens***
Petioles absent or deciduous with leaves; leaves simple or imparipinnate; anthers approximately equal or antisepalous anthers much larger than antipetalous anthers.......................................3
3. Leaves simple...4
Leaves imparipinnate...6
4. Inflorescence terminal, often also in upper axils........series ***Boronia***
Inflorescence axillary...5
5. Leaf margin smooth (Qld, NSW)..............................series ***Boronia***
Leaf margin crenulate (SW Austr.).....................series ***Heterandrae***
6. Inflorescence axillary, or axillary and terminal, 1–40^{+}-flowered; peduncle up to 30 mm long; antisepalous and antipetalous anthers approximately equal (SA, Qld, NSW, Vic., Tas.)......series ***Boronia***
Flowers axillary, solitary or in pairs, or rarely in threes; peduncle absent or minute; antisepalous approximately equal to or significantly larger than antipetalous anthers (SW Austr.)..................... ....series ***Heterandrae***

Boronia Sm. [section *Boronia*] series *Boronia*

Type: *Boronia pinnata* Sm.

Boronia series *Octarrhena* F.Muell., *Pl. Victoria* 1: 113 (1862). *Type*: *Boronia pinnata* Sm.

Boronia series *Pinnatae* Benth., *Fl. Austral.* 1: 309, 317 (1863); *Boronia* section *Pinnatae* (Benth.) De Wild., *Icon. Select.* 2: 67 (1901). *Type*: *Boronia pinnata* Sm.

Leaves imparipinnate or simple, sessile or with petiole falling with lamina. Inflorescence axillary or terminal, 1–40^{+}-flowered; peduncle up to 30 mm long. Staminal filaments pilose, puberlous or glabrous; anthers approximately equal.

A series of 21 species restricted to south-eastern Australia, including Tasmania: *Boronia citrata*, *B. citriodora* Gunn ex Hook.f. (three subspecies), *B. deanei* (two subspecies), *B. elisabethiae* Duretto, *B. falcifolia*, *B. filifolia*, *B. floribunda*, *B. galbraithiae*, *B. gunnii* Hook.f., *B. hemichiton* Duretto, *B. hippopala* Duretto, *B. imlayensis*, *B. latipinna* J.H.Willis, *B. microphylla*, *B. muelleri*, *B. pilosa* Labill. (four subspecies), *B. pinnata*, *B. rivularis* C.T.White, *B. safrolifera* Cheel, *B. serrulata*, and *B. subulifolia* Cheel.

Boronia [section *Boronia*] series *Heterandrae* Benth., *Fl. Austral.* 1: 308, 320 (1863)

Boronia section *Heterandrae* (Benth.) Engl., *Nat. Pflanzenfam.* 3(4): 136 (1896); *Boronia* section *Heteroboronia* Kuntze in T. von Post & O.Kuntze, *Lex. Gen. Phan.* 74 (1903), *nom. ille.g.* *Type*: *Boronia megastigma* Nees ex Bartl.

Leaves imparipinnate or simple; sessile or with petiole falling with lamina. Inflorescence axillary; 1- or 2(3)-flowered;

peduncle absent or minute. Staminal filaments pilose or glabrous; anthers approximately equal or antisepalous anthers much larger than antipetalous anthers.

A series of 10 species confined to south-western Australia: *Boronia clavata* (2 subspecies), *B. crassipes* Bartl., *B. gracilipes*, *B. heterophylla*, *B. megastigma*, *B. molloyae*, *B. pulchella*, *B. stricta*, and *B. virgata*.

Boronia [section *Boronia*] series *Persistens* Duretto & Heslewood, ser. nov.

Type: *Boronia purdieana* Diels.

Differs from the other series of section *Boronia* by have petioles that are persistent or tardily caducous and falling after the lamina has fallen (*v*. absent, or deciduous with lamina).

Leaves imparipinnate; petiole persistent or tardily caducous and then after lamina has fallen. Inflorescence axillary, 1- or 2-flowered; peduncle absent or minute. Staminal filaments pilose or puberulous; anthers approximately equal or antisepalous anthers much smaller than antipetalous anthers.

A series of six species confined to south-western Australia: *Boronia albiflora*, *B. crassifolia*, *B. oxyantha* (two varieties), *B. octandra*, *B. purdieana* (two subspecies), and *B. tetrandra*.

Etymology

The series epithet is derived from the Latin *persistens*, alluding to the persistent petioles that remain on the branches after the leaves have fallen.

Boronia [section *Boronia*] series *Variabiles* Benth., *Fl. Austral.* 1: 309, 320 (1863)

Type: *Boronia crenulata* Sm.

Boronia series *Terminales* Benth., *Fl. Austral.* 1: 310, 323 (1863); *Boronia* section *Terminales* (Benth.) F.Muell., *Fragm.* 9: 115 (1875). *Type*: *Boronia capitata* Sm.

Leaves simple; sessile or with petiole falling with lamina. Inflorescence axillary or terminal, flowers solitary or in small cymes; peduncle absent or minute. Staminal filaments woolly; anthers approximately equal.

A series of three species confined to south-western Australia: *Boronia capitata* (three subspecies), B. *crenulata* (four subspecies, typical subspecies with two varieties), and *B. nematophylla*.

Boronia section *Corynophyllae* Duretto & Heslewood, sect. nov.

Type: *Boronia corynophylla* Paul G.Wilson.

Differs from sections *Algidae* and *Alatae* by having simple leaves (*v*. imparipinnate or bipinnate) and exfoliating branchlets (*v*. smooth).

Hairs simple. Branches, including cortex, not articulated (continuous) at nodes, smooth and not obviously glandular, scarcely puberulous, with exfoliating cuticle that gives the branches a glaucous appearance. Leaves opposite–decussate, simple. Inflorescence terminal, 1(2 or 3)-flowered; peduncle absent or minute; bracts and bracteoles persistent. Sepals imbricate in bud; persistence unknown. Petals valvate in bud, multiveined from base, without a subterminal apiculum on abaxial surface; persistence unknown. Staminal filaments pilose, swollen and verrucose towards apex, with tip appearing subterminal adaxially. Stigma minute, as wide as or slightly wider than style. Seed not seen.

A monotypic section confined to south-western Australia.

Boronia section *Inornatae* Duretto & Heslewood, sect. nov.

Type: *Boronia inornata* Turcz.

Differs from the other sections of *Boronia* by the having the following combination of characters: glandular, verrucose branchlets, 3(5)-foliolate leaves, a terminal inflorescence of 1(–3) flowers, imbricate sepals, imbricate petals, glabrous stamens, and seeds that are microscopically tuberculate.

Hairs simple. Branches, including cortex, not articulated (continuous) at nodes, glandular–verrucose. Leaves opposite–decussate, imparipinnate. Inflorescence terminal, 1(–3)-flowered; peduncles absent; bracts and bracteoles persistent. Sepals imbricate in bud, persistent. Petals imbricate in bud, without or with a minute subterminal apiculum on the abaxial surface, multiveined from base, caducous. Staminal filament glabrous, swollen and verrucose towards apex, with tip terminal. Stigma minute, not wider than style. Seed minutely tuberculate, glossy; hilum adaxial, linear, not in a groove; embryo unknown.

A section of two species: *Boronia coriacea* (SW WA), *B. inornata* (SW WA, SA; two subspecies).

Boronia section *Ovatae* (Paul G.Wilson) Duretto & Heslewood, comb. nov., stat. nov.

Boronia series *Ovatae* Paul G.Wilson, *Nuytsia* 1: 204 (1971). *Type*: *Boronia ovata* Paul G.Wilson.

Hairs simple. Branches, including cortex, not articulated (continuous), obviously glandular, glabrous, puberulous or pilose. Leaves opposite–decussate, simple. Inflorescence a terminal cyme, cymes and solitary flowers sometimes also in axils of upper leaves; peduncle present, sometimes minute; bracts and bracteoles persistent. Sepals imbricate in bud, persistent. Petals imbricate in bud, with or without a subterminal apiculum on the abaxial surface, multiveined from base or with a single vein, caduous. Staminal filaments glabrous or pilose, swollen and verrucose towards apex, with tip appearing subterminal adaxially. Stigma minute, scarcely wider than style. Seed with a smooth sclerotesta or minutely tuberculate, cell walls not usually visible, glossy; adaxial surface with linear hilum in a groove, or with a glossy cover to the raphe; embryo unknown.

A section of three species confined to south-western Australia: *Boronia humifusa*, *B. ovata*, and *B. scabra* (three subspecies). *Boronia humifusa* has several unique features such as the petals having a single vein, a massive stigma and style, and a unique seed morphology (Wilson 1998).

Supplementary material

Supplementary material is available online.

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Data availability. New sequence data for this study are available from GenBank https://www.ncbi.nlm.nih.gov/genbank/: *ITS* OP653792–OP653880, *ETS* OP654199–OP654291, *rbc*L OP654292–OP654297, *psb*A–*trn*H OP654298–OP654390, *trn*L–*trn*F OP654391–OP654466. Alignment files are available in the Supplementary material, 'Supplementary sequence' section. Other data that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of interest. M. Bayly is an editor for *Australian Systematic Botany*. Despite this relationship, he did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Australian Systematic Botany* encourages its editors to publish in the journal and has protocols that keep editors separate from the decision-making processes for their manuscripts. The authors declare that they have no other conflicts of interest.

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