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## Comparative seed morphology of *Boronia* and related genera (Boroniinae: Rutaceae) and its systematic implications

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Comparative seed morphology of *Boronia* Sm., *Boronella* Baill., *Neobyrnesia* J. A. Armstr. and *Zieria* Sm., 31 taxa in total, in Rutaceae is studied. The seeds are ventrally ellipsoid to ovoid ( $0.93\text{--}4.42 \times 0.50\text{--}2.31 \times 0.95\text{--}2.70$  mm). Colour is brown to black. An elaiosome which is related to myrmecochory was observed in *Boronella*, *Boronia*, *Neobyrnesia* and *Zieria*. Six testa surface pattern types are identified: Type I (*Boronia* sect. *Boronia*) – smooth, and cells not barely discernable; Type II (*Boronella*) – smooth and cells more or less rectangular and often cells elongated; Type III (*Boronia* sects. *Boronia*, *Cyanothamnus*, *Imbricatae* and *Valvatae*, *Neobyrnesia*) – colliculate with four subtypes by presence, absence of ridges or ridge characters; Type IV (*Boronia* sect. *Alatae*) – digit form; Type V (*Boronia* sect. *Algidae*) – alveolate; Type VI (*Zieria*) – ridged, the interridge area formed by both cells that form the ridges and cells that do not form the ridges. Seed morphology, especially testa surface patterns, was partially congruent with the current classification of *Boronia*, with most sections having apomorphies, and provided additional support for the placement of *Boronella* near *Boronia* sect. *Boronia*. Hilum (surrounded by labiose margin or not) and elaiosome shape also offer useful diagnostic characters for *Boronia* at infrageneric levels. *Neobyrnesia* and *Zieria* both had unique testa surface patterns. The seed morphological data contribute to our understanding of systematic relationship in the subtribe Boroniinae.

Rutaceae are a nearly cosmopolitan family that includes 154 genera and approximately 2,100 species (Kubitzki et al. 2011). It is an economically important family which includes *Boronia* Sm. and *Citrus* L. (Chase et al. 1999, Groppo et al. 2008, Kubitzki et al. 2011). The family is currently divided into three subfamilies, Rutoideae, Aurantioideae and Cneoroideae (Kubitzki et al. 2011). As recent studies have indicated that the infrafamilial classification of Rutaceae is unnatural, Kubitzki et al. (2011), instead of tribes and subtribes, use informal ‘Alliances and Groups’. Subfamily Rutoideae contains tribe Boronieae, which was called the *Boronia* Alliance by Kubitzki et al. (2011). Tribe Boronieae includes 18 genera and approximately 390 species, and may prove to be polyphyletic (Groppo et al. 2008, Kubitzki et al. 2011).

According to Engler (1931), Boronieae is divided into five subtribes, and in the subtribe Boroniinae he included *Acradenia* Kippist, *Boronella* Baill., *Boronia* Sm., *Myrtopsis* Engl., *Zieria* Sm. and *Zieridium* Baill. (= *Picrella* Baill.) (Table 1). The circumscription of this subtribe is, however, problematic (Hartley 1977, 1995, Armstrong and Powell 1980, Groppo et al. 2008, Kubitzki et al. 2011, M. Bayly pers. comm.). Hartley (1977, 1995) removed *Acradenia*, *Boronella*, *Myrtopsis* and *Zieridium* from the subtribe. Kubitzki et al. (2011) placed *Acradenia* in the *Bosistoa* Alliance and the remaining three genera in the *Euodia* Alliance. Kubitzki et al. (2011) included

*Boronia*, *Zieria* and *Neobyrnesia* J. A. Armstr. in the *Boronia* Group, one of three groups in their *Boronia* Alliance.

The position of the genus *Boronella* has been controversial. Weston et al. (1984), in their cladistic analysis based on morphological data, showed that *Boronia* was paraphyletic with respect to *Boronella* and indicated that the latter should be synonymised. However, Hartley (1995) argued that *Boronella* should be retained as Weston et al. (1984) did not take embryo shape into account. The phylogenetic relationship of these genera is part of an ongoing study (M. Bayly pers. comm.). Kubitzki et al. (2011) place *Boronella* in the Rutoideae but in the *Euodia* alliance.

As currently circumscribed, *Boronia* (148 spp.) and *Neobyrnesia* (1 sp.) are endemic to Australia. *Boronia* is widespread and found in all states (Wilson 1998, Duretto 1999, 2003; Appendix 1) and *Neobyrnesia* is confined to a small area on the Arnhem Land Plateau in The Northern Territory (Armstrong and Powell 1980). *Zieria* (ca. 60 spp.) is confined to eastern Australia, apart from one species, *Z. chevalieri*, which is confined to New Caledonia (Armstrong 2002, Duretto and Forster 2007). *Boronella* (6 spp.) is endemic to New Caledonia (Hartley 1995, Kubitzki et al. 2011). Many species in these genera, including many in this study, are restricted species of high conservation value (see discussions under individual species in Armstrong and

Table 1. Subtribal classification systems and generic composition of Boroniinae/Boronia Group.

	Engler (1931)	Hartley (1977)	Armstrong and Powell (1980)	Hartley (1995)	Kubitzki et al. (2011)
Tribe Boronieae					<i>Boronia</i> Alliance
Subtribe Boroniinae					<i>Boronia</i> Group
	<i>Acradenia</i>	Moved to Zanthoxyleae	n.i.	n.i.	To <i>Bosistoa</i> Alliance
	<i>Boronella</i>	<i>Boronella</i>	Questioned placement in Boronieae	Excluded from Boronieae	To <i>Euodia</i> Alliance
	<i>Boronia</i>	<i>Boronia</i>	<i>Boronia</i>	<i>Boronia</i>	<i>Boronia</i>
	n.i.	n.i.	<i>Neobyrnnesia</i>	<i>Neobyrnnesia</i>	<i>Neobyrnnesia</i>
	<i>Myrtopsis</i>	<i>Myrtopsis</i>	Questioned placement in Boronieae	Excluded from Boronieae	To <i>Euodia</i> Alliance
	<i>Zieria</i>	<i>Zieria</i>	<i>Zieria</i>	<i>Zieria</i>	<i>Zieria</i>
	<i>Zieridium</i> (= <i>Picrella</i> )	<i>Zieridium</i> (= <i>Picrella</i> )	Questioned placement in Boronieae	Excluded from Boronieae	To <i>Euodia</i> Alliance

n.i.: not indicated.

Powell 1980, Wilson 1998, Duretto 1999, 2003, Armstrong 2002, Duretto and Forster 2007).

*Boronella* is characterised by branchlets with articulated cortex, and elliptic and suborbicular cotyledons (Hartley 1995). *Neobyrnnesia* is characterised by simple leaves, narrow, entire disk, and four and persistent stamens (Armstrong and Powell 1980, Armstrong 2002). *Zieria* is characterised by floral discs with prominent ante-staminal lobes (Armstrong 2002). Armstrong (2002) identified six natural groups in *Zieria* based on a cladogram produced from morphological data. However, the genus does not have a formal infrageneric classification.

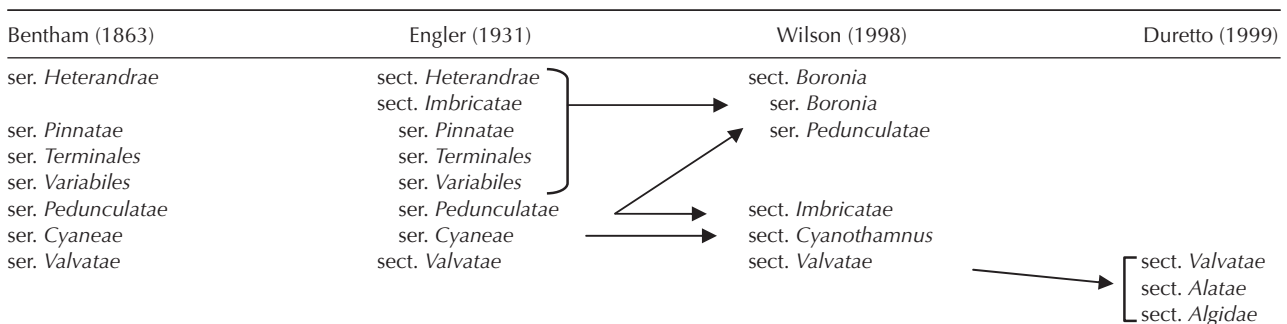
*Boronia* is characterised by opposite-decussate leaves, tetramerous flowers (usually white or pink) and eight stamens (Wilson 1998, Duretto 2003). The infrageneric classification of *Boronia* has had a complicated history (see Wilson 1971, 1998, Hartley 1995, Duretto 1999, 2003; Table 2). Bentham (1863) divided *Boronia* into seven series. Engler (1931) divided it into three sections, one of which further classified into five series. Wilson (1998), adopting some of the outcomes of Weston et al. (1984), divided the genus into four sections, with sect. *Boronia* containing two series. Duretto and Ladiges (1999) and Duretto (1999) proposed that sect. *Valvatae* be divided into three sections and erected sects. *Algidae* and *Alatae* as well as describing a complex infrasectional classification for the section. Currently, six sections are recognised within *Boronia* (Table 2). Though published cladistic analyses of the genus (Weston et al. 1984) or sect. *Valavatae* (Duretto and Ladiges 1999) indicate that all sections are monophyletic, the relationship among them is not well understood. Section

*Boronia*, and in particular, ser. *Boronia*, may yet prove to be paraphyletic with respect to other sections and *Boronella* (M. Bayly, M. Duretto unpubl. data) confirming, in part, the results presented by Weston et al. (1984).

In *Boronia*, *Boronella*, *Neobyrnnesia* and *Zieria* the individual carpels contain two ovules though one usually aborts before the seed matures thus there is usually one seed per follicle (Armstrong and Powell 1980, Hartley 1995, Armstrong 2002, Duretto 2003). Mature seeds of these genera, as with all members of the *Boronia* Alliance and many other genera in Rutaceae, are ejected from follicles explosively by an elastic endocarp (see Armstrong and Powell 1980, Armstrong 2002, Duretto 1999, 2003). Seeds of Boroniinae are brown to black, and have ellipsoid, linear or thin hilum, and often have thick or membranaceous elaiosome (Armstrong and Powell 1980, Wilson 1998, Duretto 1999, Kubitzki et al. 2011). Some species of *Zieria* and *Boronia* are reported to be myrmecochorous (e.g. *Z. laevigata*, *B. parviflora*) having an ant-attracting elaiosome (Rice and Westoby 1981, Armstrong 2002). Heat and fire were reported to be related to the seed germination in some *Boronia* and *Zieria* species (e.g. *Boronia ledifolia*, *B. serrulata*, *Zieria arborescens*, *Z. laevigata*; Auld 2001). In addition, smoke was also reported to be related to breaking the seed dormancy of some *Boronia* species in Australian Rutaceae (Dixon et al. 1995, Roche et al. 1997).

Seed morphological characters have proven to be important in the systematics of angiosperms at various taxonomic levels (Barthlott 1981, 1984, Werker 1997, Vural et al. 2008). In Rutaceae, seed morphological studies have been conducted in Aurantioideae and Rutoideae and seed shape,

Table 2. Infrageneric classification systems of *Boronia*.



seed coat morphology and seed coat layers provided taxonomic information (Liu et al. 1997, Hamilton et al. 2008). Seed morphological characters have also been used in subtribe *Boroniinae* (e.g. testa surface pattern in *Neobyrnesia*, hilum characters in sect. *Boronia*; Armstrong and Powell 1980, Wilson 1998). Seed morphology of *Boronia* and related genera has been studied by several researchers over the last three decades (Table 3), however most data in earlier studies is fragmented with studies covering selected species or sections, or at a broader level at series or sectional level (e.g. Wilson 1998). Seeds are often generally described in taxonomic revisions (e.g. Duretto 1997, 1999, 2003, Duretto and Forster 2007), or only key features or traits are described, for example, for scoring characters for cladistic analyses (Weston et al. 1984, Duretto and Ladiges 1999), or defining specific infrageneric taxa (e.g. Wilson 1998, Duretto 1999). Powell and Armstrong (1980) describe and illustrate the testa surface patterns of *Zieria* and classify 23 species into three major groups and some subgroups. Later, when revising the genus, Armstrong (2002) describes and illustrates the seed surface of most taxa. When describing *Neobyrnesia* Armstrong and Powell (1980) describe and illustrate the seed surface of the sole species.

However, seed morphological characters including testa surface patterns (SEM analysis), seed size, shape, hilum and elaiosome characters still need to be studied and described for many taxa (Table 3). Compared with previous research, the current study is not only more comprehensive in that morphological characters are more comprehensively covered but also because it utilised a wider range of methods, including SEM analysis of testa surface patterns and seed coat layer thickness, as well as mapping testa surface pattern characters onto recent phylogenies.

The aim of this study is 1) to describe seed morphological characters in detail for selected taxa in *Boronella*, *Boronia*, *Zieria* and *Neobyrnesia*, 2) to test the usefulness of seed characters in distinguishing various taxonomic groups and 3) to verify if seeds provide any evidence of the infrageneric and intergeneric relationship among the four genera.

## Material and methods

The study is based on herbarium material from BRI, CANB, HO, MEL, NOU (acronyms follow Holmgren et al. 1990; see Appendix 1). A total of 31 taxa from *Boronia* and related genera were selected. For *Boronia*, 23 taxa across all six sections and the two series in section *Boronia* were studied. In *Boronia*, taxa that previously were not described or not thoroughly described were included. In *Zieria*, six taxa from each of the six major groups identified by Armstrong (2002) were selected. In the monotypic genus *Neobyrnesia*, *N. suberosa* was studied. For *Boronella*, only material of *Boronella crassifolia* was available for study.

To determine shape and size, seeds were examined under light microscope (Stereo Discovery V8, Carl Zeiss, Jena). On average, five-ten seeds per taxon were measured, and in seven taxa (*Boronella crassifolia*, *Boronia grandisepala* subsp. *acanthophida*, *B. algida*, *B. anethifolia*, *Neobyrnesia suberosa*, *Zieria minutiflora* subsp. *minutiflora*, *Z. smithii*

subsp. *smithii*), two to three seeds per taxon were available only. We included these taxa for comparative reasons although we did not obtain sufficient material.

Three characters were measured for 128 samples (28 taxa): length, width and thickness. Seed length was measured along the longest axis in the hilum plane, width at the vertical angle to the hilum plane, and thickness along the dorsal and ventral plane (following Denk and Oh 2006). Minimum (average) maximum sizes of each taxon investigated are presented in Table 5. Colour was measured against The Royal Horticultural Society Colour Chart\*. In all the cases, only seeds that were solitary in the follicle were measured except *Boronella crassifolia* (where seeds were observed in pairs). As only immature material was available for *Boronia baeckeacea* subsp. *baeckeacea*, *Boronia coerulescens* subsp. *spinescens* and *Boronia cymosa*, complete seed morphological data for these taxa is not provided, except mainly for testa surface pattern type. Some seed morphological data was sourced from Armstrong and Powell (1980), Duretto (1999) and Wilson (1998) (Table 5).

For the SEM analysis, selected seeds were directly mounted on aluminium stubs using double sided or carbon tape with carbon paint. Specimens were then coated with platinum using a JFC-1100E ion sputter coater, and examined and photographed at 20kV with a JEOL JSM-5200 (JEOL, Tokyo). Methodology of SEM analysis followed Hong (1993) and Moon and Hong (2006). For testa surface patterns, central parts of lateral sides of seeds were studied using SEM or LM. Testa surface pattern types are divided by cell shape, ridge and interridge formation characters. In transverse section, lateral central part of a seed was dissected. The size measurements of exostesa, mesotesta and endotesta on SEM were made using Carnoy 2.0 (Schols et al. 2002). The size measurements of exotesta includes the epidermis. The terminology of the seed external morphology in general follows Wilson (1998), Duretto and Ladiges (1999), Armstrong (2002) and Denk and Oh (2006).

## Results

Seed morphological characters (size, colour, shape, luster, hilum shape, the presence/absence, texture and shape of elaiosome, testa surface pattern and seed coat layer thickness) are summarised in Table 5–6. Representative micrographs of the investigated taxa are shown in Fig. 1–4. Testa surface pattern types are summarised in Table 4.

In *Boronia* and related taxa, seed are laterally ellipsoid, ovoid, or kidney shaped, ventrally, ellipsoid or ovoid and transverse sectional shapes are ellipsoid or ovoid. Seed size is  $0.93\text{--}4.42 \times 0.50\text{--}2.31 \times 0.95\text{--}2.70$  mm long (length  $\times$  width  $\times$  thickness). Seed colour is brown, dark brown, shiny grey or black. Seeds are dull or shiny. Hilum shape is ellipsoid, ovoid, trullate to linear and surrounded by labiose margin or not. Elaosome is present or absent. Elaosome texture is membranaceous, fleshy on lower central and membranaceous on upper and lateral margin or thick. Elaosome shape is ellipsoid, ovoid, fusiform, trullate or heart shaped. Elaosome colour is white, ivory, light brown or dark brown. Testa surface patterns are classified into Types

Table 3. Overview of previous seed morphological studies in *Boronia*, *Boronella*, *Neobyrnesia* and *Zieria* of the investigated taxa in this study.

Taxon	Seed size	Colour	Shape		Luster	Elaiosome	Testa pattern (SEM analysis)	References
			Seed	Hilum				
<i>Boronia</i>								
sect. <i>Alatae</i>								
<i>B. alata</i>	-	+	+	+	+	+	+	Wilson (1998), under section <i>Valvatae</i> ; Duretto (1999); Duretto and Ladiges (1999)
sect. <i>Algidae</i>								
<i>B. algida</i>	-	+	+	+	+	+	+	Duretto (1999); Duretto and Ladiges (1999)
sect. <i>Boronia</i>								
ser. <i>Boronia</i>								
<i>B. falcifolia</i>	+	+	-	-	-	-	-	Duretto (2003)
<i>B. gunnii</i>	-	-	-	-	-	-	-	-
<i>B. pilosa</i> ssp. <i>pilosa</i>	+	-	-	-	-	-	-	Duretto (2003)
<i>B. pinnata</i>	+	-	-	-	-	-	-	Duretto (2003)
<i>B. scabra</i> ssp. <i>scabra</i>	-	+	+	+	-	+	-	Wilson (1998), at series level
<i>B. thujona</i>	+	+	-	-	-	-	-	Duretto (2003)
ser. <i>Pedunculatae</i>								
<i>B. parviflora</i>	+	+	+	+	-	+	+	Wilson (1998), at series level; Duretto (2003)
sect. <i>Cyanothamnus</i>								
<i>B. anemonifolia</i>								
ssp. <i>variabilis</i>	-	-	-	-	-	-	-	-
<i>B. anethifolia</i>	+	+	-	-	+	-	+	Duretto (2003)
<i>B. baeckeacea</i>								
ssp. <i>baeckeacea</i>	-	-	-	-	-	-	-	-
<i>B. busselliana</i>	-	-	-	-	-	-	-	-
<i>B. coerulescens</i>								
ssp. <i>spinescens</i>	-	-	-	-	-	-	-	-
<i>B. occidentalis</i>	+	+	-	-	+	-	+	Duretto (2003)
<i>B. ramosa</i>								
ssp. <i>anethifolia</i>	-	-	-	-	-	-	-	-
sect. <i>Imbricatae</i>								
<i>B. cymosa</i>	-	+	+	+	-	+	-	Wilson (1998)
sect. <i>Valvatae</i>								
<i>B. alulata</i>								
	+	-	+	-	+	-	+	Duretto (1998, 1999); Duretto and Ladiges (1999)
<i>B. bowmanii</i>	+	-	+	-	-	-	+	Duretto (1998, 1999); Duretto and Ladiges (1999)
<i>B. grandisepala</i>	+	+	+	-	+	+	+	Duretto and Ladiges (1997, 1999); Duretto (1999)
ssp. <i>acanthophida</i>	-	-	+	-	+	-	+	Duretto (1998, 1999)
<i>B. obovata</i>	+	+	-	-	+	+	+	Duretto (1998, 1999)
<i>B. warrumbunglensis</i>	-	-	+	-	+	-	+	Duretto (1999); Duretto and Ladiges (1999)
<i>Boronella</i>								
<i>B. crassifolia</i>	-	-	-	-	-	-	-	-
<i>Neobyrnesia</i>								
<i>N. suberosa</i>	-	-	-	+	-	+	+	Armstrong and Powell (1980)
<i>Zieria</i>								
<i>Z. arborescens</i>								
ssp. <i>arborescens</i>	+	+	-	-	-	-	+	Powell and Armstrong (1980); Armstrong (2002)
<i>Z. furfuracea</i>								
ssp. <i>euthadenia</i>	+	+	-	-	-	-	+	Powell and Armstrong (1980); Armstrong (2002)
<i>Z. laevigata</i>	+	+	-	-	-	-	+	Powell and Armstrong (1980); Armstrong (2002)
<i>Z. minutiflora</i>								
ssp. <i>minutiflora</i>	+	+	-	-	-	-	+	Powell and Armstrong (1980); Armstrong (2002)
<i>Z. smithii</i> ssp. <i>smithii</i>	+	+	-	-	-	-	+	Powell and Armstrong (1980); Armstrong (2002)
<i>Z. veronicea</i>								
ssp. <i>veronicea</i>	+	+	-	-	-	+	+	Powell and Armstrong (1980); Armstrong (2002)

Table 4. Summary of testa surface pattern types of *Boronella*, *Boronia*, *Neobyrnesia* and *Zieria*.

Type	Description of seed coat surface
I	smooth, and cells not barely discernable
II	smooth and cells more or less rectangular and often cells elongated
III	colliculate
IIIa	cells distinct, not fused
IIIb	ridged, ridges linear and constructed of a row of completely fused cells, the interridge area formed of the same cells that form the ridges
IIIc	ridged, ridges linear and constructed of a row of partially fused cells, the interridge area formed of the same cells that form the ridges
IIId	ridged but ridges are rare, cells irregularly fused
IV	digit form
V	alveolate
VI	ridged, the interridge area is formed by both cells that form the ridges and cells that do not form the ridges, and interridge area is variously patterned

I–VI (Table 4, Fig. 5E–F), in Type IIIa, sometimes hilly protrusions or rarely reticulate pattern is observed (Fig. 1H–L, 3C). The testa surface pattern types are divided by whether testa is smooth (Type I) or not (Type III, IV, V), and Type III was subdivided by presence, absence or rarity of ridges or ridge characters. When the smooth testa had more or less discernable rectangular cells, Type II was given. When ridged, and the interridge includes cells other than the ridge cells, Type VI was assigned (see Table 4). Testa thickness as follows: exotesta 4.50–68.47  $\mu\text{m}$  thick, mesotesta (sclerenchymatous layer) 34.62–203.93  $\mu\text{m}$  thick, and endotesta 3.13–17.19  $\mu\text{m}$  thick.

***Boronia* (Fig. 1B–O, 2A–C, 2E–O, 2Q–S, 3A–D, 4B–D, Table 5–6)**

Seeds laterally and ventrally ellipsoid to ovoid, in transverse section (t.s.), ellipsoid;  $0.93\text{--}4.42 \times 0.50\text{--}2.31 \times 0.98\text{--}2.70$  mm long, the smallest in sect. *Boronia* (*B. parviflora*), the largest in sect. *Valvatae* (*B. warrumbunglensis*). Hilum ellipsoid (Fig. 1F) to linear (e.g. Fig. 1B). Elaiosome present or absent; membranaceous to thick; ellipsoid to trullate; white to dark brown. Testa shiny or rarely dull; brown to black. Testa surface patterns characterised by four types and three subtypes (Types I, IIIa–b, d, IV–V), sometimes with hilly protrusions in sects. *Cyanothamnus* and *Imbricatae*, and rarely reticulate pattern is observed in sect. *Cyanothamnus*; thickness as follows: exotesta 8.07–59.47  $\mu\text{m}$  thick, mesotesta 43.90–203.93  $\mu\text{m}$  thick, and endotesta 3.14–17.19  $\mu\text{m}$  thick (Fig. 4B–D, Table 6).

***Boronia* section *Alatae* (Fig. 1B, 2R, 3A, 4B, Table 5–6)**

Seeds laterally ellipsoid and ventrally ovoid, in t.s., ellipsoid;  $2.70\text{--}2.86 \times 1.43\text{--}1.55 \times 1.91\text{--}2.07$  mm long. Hilum linear. Elaiosome present; thick. Testa dull; brown. Testa surface pattern Type IV (digit form; Fig. 2R), thickness as follows: exotesta 17.34–58.20  $\mu\text{m}$  thick, mesotesta 170.71–203.93  $\mu\text{m}$  thick, and endotesta 3.91–8.93  $\mu\text{m}$  thick (Fig. 4B, Table 6).

–Taxon examined: *B. alata*.

***Boronia* section *Algidae* (Fig. 1C, 2S, 3B, 4C, Table 5–6)**

Seeds laterally ovoid with hilar side flattened and ventrally ovoid, in t.s., ellipsoid;  $2.49\text{--}2.69 \times 0.90\text{--}1.00 \times 1.17\text{--}1.23$  mm long. Hilum linear. Elaiosome present. Testa dull; dark brown. Testa surface pattern Type V (alveolate; Fig. 2S), thickness as follows: exotesta 10.44–33.59  $\mu\text{m}$  thick, mesotesta 58.06–85.16  $\mu\text{m}$  thick, and endotesta 10.54–14.45  $\mu\text{m}$  thick (Fig. 4C, Table 6).

–Taxon examined: *B. algida*.

***Boronia* section *Boronia* (Fig. 1D–G, 2A–C, 2I, 3D, Table 5–6)**

Seeds laterally ellipsoid to ovoid and flattened, ventrally ellipsoid to ovoid, in t.s., ellipsoid;  $0.93\text{--}2.80 \times 0.50\text{--}1.10 \times 0.98\text{--}1.75$  mm long. Hilum mostly linear (Fig. 1E) or rarely ellipsoid (short; Fig. 1F), sunken surrounded by labiose margin (Fig. 1E–F) or not (Fig. 1G). Elaiosome present or absent; white; membranaceous and caducous; ellipsoid. Testa shiny; black, rarely brown or dark brown. Testa surface pattern mostly Type I (smooth, and cells not barely discernable; Fig. 2A–Ba, 2C) and rarely Type IIIa (colliculate – cells distinct, not fused; Fig. 2I). Testa thickness as follows: exotesta 12.76–30.21  $\mu\text{m}$  thick, mesotesta 49.62–74.30  $\mu\text{m}$  thick, and endotesta 3.92–17.19  $\mu\text{m}$  thick (Table 6).

***Boronia* section *Boronia* series *Boronia* (Fig. 1D–F, 2A–C, 2I, 3D, Table 5–6)**

Seeds laterally ellipsoid to ovoid and flattened, ventrally ellipsoid to ovoid, in t.s., ellipsoid (*B. pinnata*);  $1.40\text{--}2.80 \times 0.50\text{--}1.10 \times 0.98\text{--}1.75$  mm long. Hilum linear (except *B. scabra* subsp. *scabra* [short: ellipsoid]), sunken surrounded by labiose margin. Elaiosome present in *B. gunnii* (Fig. 1D) and in *B. scabra* subsp. *scabra* (Table 5) or absent; in *B. gunnii*, ellipsoid, in the center, white, membranaceous and caducous. Testa shiny; mostly black to rarely brown (*B. scabra* subsp. *scabra*). Testa surface pattern mostly Type I (smooth, and cells not barely discernable; Fig. 2A, 2Ba, 2C) except *B. scabra* subsp. *scabra* (Type IIIa: colliculate – cells distinct, not fused; Fig. 2I). Testa surface pattern of lateral basal part of *B. pilosa* subsp. *pilosa* (Fig. 2Bb) has vaguely rectangular cells (the cells often elongated). Testa thickness as follows: exotesta 12.76–30.21  $\mu\text{m}$  thick, mesotesta 58.14–74.30  $\mu\text{m}$  thick, and endotesta 7.87–17.19  $\mu\text{m}$  thick (Table 6).

–Taxa examined: *B. falcifolia*, *B. gunnii*, *B. pilosa* subsp. *pilosa*, *B. pinnata*, *B. scabra* subsp. *scabra*, *B. thujona*.

***Boronia* section *Boronia* series *Pedunculatae* (Fig. 1G, Table 5–6)**

Seeds laterally ellipsoid and flattened, ventrally ovoid, in t.s., ellipsoid;  $0.93\text{--}1.61 \times 0.75\text{--}0.80 \times 1.01\text{--}1.20$  mm long. Hilum linear, not sunken and not surrounded by labiose margin (Fig. 1G). Raphe pulpy at the base of seed. Elaiosome present, membranaceous and caducous (Table 5). Testa shiny; black. Testa surface pattern Type I (smooth, and cells not barely discernable); thickness as follows: exotesta

Table 5. Seed morphological characters examined in *Boronia*, *Boronella*, *Neobyrnnesia* and *Zieria*. C (colour) – b: brown with brownish grey spots, c: black, g: black with grey area, r: brown, w: dark brown, z: shiny grey marked with black spots, El (elaiosome) – A (elaiosome shape): see shape, P: presence – a: absent, p: present, Te: texture – i: thin, j: fleshy on lower central and membranaceous on upper and lateral margin, m: membranaceous, t: thick, H (hilum shape): see shape, Shape (Cr: transverse sectional, L: lateral, V: ventral.) – e: ellipsoid, f: fusiform, h: heart shaped, k: kidney shaped, l: linear, o: ovoid, x: trullate, Testa pattern (testa surface pattern) – Types I–VI (see Table 4), U (luster) – d: dull, s: shiny, -: lack of information, \*: data adopted from Armstrong and Powell (1980), Wilson (1998) or Duretto (1999).

Taxon	Size (mm); min (average) max			Shape						El			Testa pattern	Figures
	Length	Width	Thickness	C	L	V	Cr	U	H	P	Te	A		
<i>Boronia</i>														
sect. Alatae														
<i>B. alata</i>	2.70 (2.77) 2.86	1.43 (1.49) 1.55	1.91 (2.00) 2.07	r	e	o	e	d	l	p*	t	–	IV	1B, 2R, 3A, 4B
sect. Algidae														
<i>B. alghda</i>	2.49 (2.59) 2.69	0.90 (0.95) 1.00	1.17 (1.20) 1.23	w	o	o	e	d	l	p*	–	–	V	1C, 2S, 3B, 4C
sect. <i>Boronia</i>														
ser. <i>Boronia</i>														
<i>B. falcifolia</i>	1.40 (1.59) 1.81	0.70 (0.77) 0.80	0.98 (1.06) 1.20	w	e	e	–	s	l	a	–	–	I	2A
<i>B. gunnii</i>	2.40 (2.54) 2.80	0.50 (0.89) 1.10	1.15 (1.24) 1.40	c	o	o	–	s	l	p	m	e	I	1D
<i>B. pilosa</i> ssp. <i>pilosa</i>	2.10 (2.30) 2.50	1.00 (1.02) 1.03	1.25 (1.39) 1.75	c	e	e	–	s	l	a	–	–	I	2Ba–Bb
<i>B. pinnata</i>	2.11 (2.35) 2.64	0.84 (0.93) 1.00	1.17 (1.31) 1.46	c	e	o	e	s	l	a	–	–	I	1E, 3D
<i>B. scabra</i> ssp. <i>scabra</i>	1.80 (2.00) 2.30	0.70 (0.80) 0.90	1.10 (1.24) 1.40	r	e	o	–	s	e	p*	m*	–	IIla	1F, 2I
<i>B. thujona</i>	2.21 (2.30) 2.40	0.81 (0.88) 1.00	1.22 (1.29) 1.40	c	e	e	–	s	l	a	–	–	I	2C
ser. <i>Pedunculatae</i>														
<i>B. parviflora</i>	0.93 (1.27) 1.61	0.75 (0.78) 0.80	1.01 (1.11) 1.20	c	e	o	e	s	l	p*	m*	–	I	1G
sect. <i>Cyanothamnus</i>														
<i>B. anemonifolia</i>	2.30 (2.42) 2.70	1.15 (1.18) 1.20	1.50 (1.51) 1.60	c	e	o	–	s	l	a	–	–	IIla	–
ssp. <i>variabilis</i>														
<i>B. anethifolia</i>	2.53 (2.67) 2.80	1.10 (1.11) 1.20	1.53 (1.55) 1.58	c	e	o	e	s	l	p	m	o	IIla	1H, 2K, 3C
<i>B. baeckeacea</i>	–	–	–	–	–	–	–	–	–	p*	m*	–	IIla	–
ssp. <i>baeckea</i>														
<i>B. busselliana</i>	3.47 (3.74) 4.00	1.80 (1.81) 1.82	2.50 (2.60) 2.70	c	e	o	e	s	x	p	m	–	IIla	1I–J, 2F, 4D
<i>B. coerulea</i>	–	–	–	–	–	–	–	–	–	p*	m*	–	IIla	2L
ssp. <i>spinescens</i>														
<i>B. occidentalis</i>	2.49 (2.59) 2.70	1.03 (1.10) 1.14	1.10 (1.20) 1.22	b	e	o	–	d	l	p	m	x	IIla	1K, 2M
<i>B. ramosa</i> ssp. <i>anethifolia</i>	3.10 (3.20) 3.40	1.15 (1.50) 1.60	1.90 (2.00) 2.10	c	e	o	–	s	l	p	m	o	IIla	1L, 2N
sect. <i>Imbricatae</i>														
<i>B. cymosa</i>	–	–	–	z*	k*	–	–	–	l*	p*	i*	o*	IIla	2G
sect. <i>Valvatae</i>														
<i>B. alulata</i>	3.00 (3.10) 3.30	1.40 (1.53) 1.70	1.00 (1.42) 1.60	c	o	o	–	s	e	p	t	f	IIla	1M, 2E
<i>B. bowmanii</i>	3.20 (3.50) 3.90	1.40 (1.60) 1.65	1.60 (1.80) 1.90	c	o	o	–	s	o	p	t	f	IIId	2Q
<i>B. grandisepala</i>	3.00 (3.20) 3.40	1.10 (1.15) 1.20	1.20 (1.43) 1.65	c	o	o	–	s	l	p	t	o	IIlb	2O
ssp. <i>acanthophida</i>														
<i>B. obovata</i>	3.75 (4.01) 4.30	1.77 (1.95) 2.31	2.00 (2.11) 2.30	c	o	o	–	s	l	p	t	f	IIla	–
<i>B. odorata</i>	3.80 (3.90) 4.10	1.30 (1.56) 1.80	1.85 (1.98) 2.08	c	o	o	–	s	l	p	t	f	IIla	1N, 2H
<i>B. warrumbunglensis</i>	4.40 (4.41) 4.42	1.90 (1.98) 2.00	2.40 (2.46) 2.51	c	o	o	e	s	l	p	t	f	IIla	1O, 2J
<i>Boronella</i>														
<i>B. crassifolia</i>	2.05 (2.08) 2.10	1.00 (1.03) 1.05	1.10 (1.13) 1.15	c	o	o	e	d	o	p	–	–	II	1A, 2D, 4A
<i>Neobyrnnesia</i>														
<i>N. suberosa</i>	3.20 (3.33) 3.45	1.40 (1.43) 1.45	1.55 (1.59) 1.62	c	e	o	e	s	l	p	j*	–	IIlc	1P, 2P, 3E, 4E

(Continued)

Table 5. (Continued)

Taxon	Size (mm); min (average) max			Thickness	Shape					El		Testa pattern	Figures		
	Length	Width	Thickness		C	L	V	Cr	U	H	P			Te	A
<i>Zieria</i>															
<i>Z. arborescens</i>	2.30 (2.36)	1.05 (1.10)	1.11	1.15 (1.53)	w	o	e	e	s	l	p	m	h	VI	1Q, 2Ta–Tb
ssp. <i>arborescens</i>															
<i>Z. furfuracea</i> ssp. <i>euthadenia</i>	2.10 (2.29)	0.90 (0.98)	1.11	1.10 (1.28)	w	o	o	e	s	l	p	m	h	VI	1R, 2U, 3F
<i>Z. laevigata</i>	3.20 (3.32)	1.28 (1.30)	1.33	1.07 (1.62)	w	o	o	o	s	l	p	m	o	VI	1S, 2Va–Vb, 3G
<i>Z. minutiflora</i> ssp. <i>minutiflora</i>	1.75 (1.83)	0.65 (0.68)	0.70	0.95 (1.04)	w	e	o	e	d	l	p	m	o	VI	2W
<i>Z. smithii</i> ssp. <i>smithii</i>	2.32 (2.41)	1.00 (1.15)	1.30	1.25 (1.28)	w	e	e	e	s	l	p	m	x	VI	2X, 4F
<i>Z. veronicea</i> ssp. <i>veronicea</i>	3.00 (3.11)	1.22 (1.34)	1.50	2.00 (2.07)	g	e	o	e	s	l	p	m	o	VI	1T, 2Y, 3H

14.67–18.50  $\mu\text{m}$  thick, mesotesta 49.62–62.53  $\mu\text{m}$  thick, and endotesta 3.92–7.26  $\mu\text{m}$  thick (Table 6).

–Taxon examined: *B. parviflora*.

### ***Boronia* section *Cyanothamnus* (Fig. 1H–L, 2F, 2K–N, 3C, 4D, Table 5–6)**

Seeds laterally ellipsoid, ventrally ovoid, in t.s., ellipsoid (*B. anethifolia*, *B. busselliana*); 2.30–4.00  $\times$  1.03–1.82  $\times$  1.10–2.70 mm long, the smallest seeds found in *B. occidentalis*, the largest in *B. busselliana*. Hilum usually linear, along the ventral side, to the base, and not surrounded by labiose margin in all the taxa examined except *B. busselliana* where trullate and surrounded by labiose margin. Elaiosomes present in all taxa examined except *B. anemonifolia* subsp. *variabilis* (Table 5), trullate or ovoid with linear shaped elaiosome attached underneath (Fig. 1H, 1L). Elaiosome white to ivory (*B. anethifolia*, *B. occidentalis*), light brown (*B. ramosa* subsp. *anethifolia*), membranaceous and usually caducous or rarely persistent (*B. ramosa* subsp. *anethifolia*). Testa shiny or rarely dull (*B. occidentalis*); mostly black to rarely brown with brownish grey spots (*B. occidentalis*); wax present in *B. occidentalis* (Fig. 2M), *B. coerulescens* subsp. *spinescens* (Fig. 2L), *B. baeckeacea* subsp. *baeckeacea*, *B. ramosa* subsp. *anethifolia* (Fig. 2N). Testa surface pattern Type IIIa (colliculate – cells distinct, not fused; Fig. 2F, 2K–N). Testa usually with hilly protrusions (Fig. 1H, 1K, 1L, 3C) or rarely with reticulate pattern (Fig. 1I–J). Testa thickness as follows: exotesta 8.07–46.45  $\mu\text{m}$  thick, mesotesta 43.90–188.33  $\mu\text{m}$  thick, endotesta 3.14–8.45  $\mu\text{m}$  thick (Fig. 4D, Table 6).

–Taxa examined: *B. anemonifolia* subsp. *variabilis*, *B. anethifolia*, *B. baeckeacea* subsp. *baeckeacea*, *B. busselliana*, *B. coerulescens* subsp. *spinescens*, *B. occidentalis*, *B. ramosa* subsp. *anethifolia*.

### ***Boronia* section *Imbricatae* (Fig. 2G, Table 5)**

Immature seeds were observed only. Seeds kidney shaped. Hilum linear. Elaiosome present, ovoid, cream coloured, thin, deciduous. Testa shiny grey marked with black spots on ridges (Table 5). Testa surface pattern Type IIIa (colliculate – cells distinct, not fused), with hilly protrusions. Outer testa membranaceous.

–Taxon examined: *B. cymosa*.

### ***Boronia* section *Valvatae* (Fig. 1M–O, 2E, 2H, 2J, 2O, 2Q, Table 5–6)**

Seeds laterally and ventrally ovoid, with laterally hilar side flattened, in t.s., ellipsoid (*B. warrumbunglensis*); 3.00–4.42  $\times$  1.10–2.31  $\times$  1.00–2.51 mm long. Hilum ellipsoid to linear. Elaiosome present in all taxa, fusiform or ovoid with linear shaped elaiosome underneath, along the ventral area. Elaiosome light brown or rarely dark brown (*B. warrumbunglensis*), usually thick and persistent. Testa shiny; black. Testa surface pattern Type III (colliculate with three subtypes):



Table 6. Measurements of seed coat layer thickness of the investigated taxa in *Boronia*, *Boronella*, *Neobyrnesia* and *Zieria* (unit:  $\mu\text{m}$ ); min (average) max.

Taxon	Exotesta*	Mesotesta	Endotesta
<i>Boronia</i>			
sect. <i>Alatae</i>			
<i>B. alata</i>	17.34 (37.80) 58.20	170.71 (183.71) 203.93	3.91 (6.01) 8.93
sect. <i>Algidae</i>			
<i>B. algida</i>	10.44 (23.22) 33.59	58.06 (73.19) 85.16	10.54 (12.35) 14.45
sect. <i>Boronia</i>			
ser. <i>Boronia</i>			
<i>B. pinnata</i>	12.76 (18.82) 30.21	58.14 (66.21) 74.30	7.87 (12.99) 17.19
ser. <i>Pedunculatae</i>			
<i>B. parviflora</i>	14.67 (16.24) 18.50	49.62 (55.84) 62.53	3.92 (5.32) 7.26
sect. <i>Cyanothamnus</i>			
<i>B. anethifolia</i>	8.07 (14.65) 20.94	43.90 (86.49) 149.96	3.14 (5.64) 7.33
<i>B. busselliana</i>	15.18 (26.92) 46.45	177.25 (181.93) 188.33	5.83 (6.81) 8.45
sect. <i>Valvatae</i>			
<i>B. warrumbunglensis</i>	37.39 (47.05) 59.47	141.59 (149.29) 170.36	7.75 (9.81) 11.77
<i>Boronella</i>			
<i>B. crassifolia</i>	7.35 (9.22) 11.49	34.62 (37.43) 45.71	3.13 (4.07) 6.04
<i>Neobyrnesia</i>			
<i>N. suberosa</i>	22.30 (26.58) 34.94	110.81 (116.65) 132.17	8.99 (10.74) 14.47
<i>Zieria</i>			
<i>Z. arborescens</i> ssp. <i>arborescens</i>	6.65 (26.19) 56.48	138.63 (146.47) 151.32	4.80 (6.05) 7.25
<i>Z. furfuracea</i> ssp. <i>euthadenia</i>	4.50 (12.63) 28.95	55.87 (72.45) 78.16	3.40 (4.32) 6.18
<i>Z. laevigata</i>	10.06 (37.71) 68.47	147.59 (151.49) 155.69	6.09 (8.55) 11.18
<i>Z. minutiflora</i> ssp. <i>minutiflora</i>	10.38 (16.30) 23.55	45.09 (48.62) 54.34	6.02 (8.09) 12.17
<i>Z. smithii</i> ssp. <i>smithii</i>	6.70 (18.74) 31.53	44.07 (53.67) 60.82	5.52 (6.96) 10.55
<i>Z. veronicea</i> ssp. <i>veronicea</i>	12.28 (23.95) 35.16	147.307 (156.31) 169.38	6.25 (8.37) 10.06

\*: the measurements of exotesta include epidermis.

Type IIIa (cells distinct, not fused) (*B. alulata*, *B. obovata*, *B. odorata*, *B. warrumbunglensis*; Fig. 2E, 2H, 2J), Type IIIb (ridged, ridges linear and constructed of a row of completely fused cells, the interridge area formed of the same cells that form the ridges) (*B. grandisepala* subsp. *acanthopsida*; Fig. 2O), Type IIIc (ridged but ridges are rare, cells irregularly fused) (*B. bowmanii*; Fig. 2Q). Testa thickness is as follows: exotesta 37.39–59.47  $\mu\text{m}$  thick, mesotesta 141.59–170.36  $\mu\text{m}$  thick, endotesta 7.75–11.77  $\mu\text{m}$  thick (Table 6).

–Taxa examined: *B. alulata*, *B. bowmanii*, *B. grandisepala* subsp. *acanthopsida*, *B. obovata*, *B. odorata*, *B. warrumbunglensis*.

### ***Boronella* (Fig. 1A, 2D, 4A, Table 5–6)**

Seeds laterally and ventrally ovoid, in t.s., ellipsoid; 2.05–2.10  $\times$  1.00–1.05  $\times$  1.10–1.15 mm long. Hilum ovoid. Elaiosome seen on an immature seed. Testa dull; black. Testa surface pattern Type II (smooth and cells more or less rectangular and often cells elongated; Fig. 2D), thickness as follows: exotesta 7.35–11.49  $\mu\text{m}$  thick, mesotesta 34.62–45.71  $\mu\text{m}$  thick, and endotesta 3.13–6.04  $\mu\text{m}$  thick (Fig. 4A, Table 6).

–Taxon examined: *B. crassifolia*.

### ***Neobyrnesia* (Fig. 1P, 2P, 3E, 4E, Table 5–6)**

Seeds laterally ellipsoid and ventrally ovoid, in t.s., ellipsoid; 3.20–3.45  $\times$  1.40–1.45  $\times$  1.55–1.62 mm. Hilum linear.

Elaiosome seen on an immature seed, fleshy on lower middle portion and membranaceous on upper and lateral margin (Table 5). Testa shiny; black. Testa surface pattern Type IIIc (colliculate – ridged, ridges linear and constructed of a row of partially fused cells, the interridge area formed of the same cells that form the ridges; Fig. 2P). In this type, colliculate cell shapes sometimes visible on the ridge as some longitudinal cells do not completely fuse to form ridges; thickness as follows: exotesta 22.30–34.94  $\mu\text{m}$  thick, mesotesta 110.81–132.17  $\mu\text{m}$  thick, endotesta 8.99–14.47  $\mu\text{m}$  thick (Fig. 4E, Table 6).

–Taxon examined: *N. suberosa*.

### ***Zieria* (Fig. 1Q–T, 2T–Y, 3F–H, 4F, Table 5–6)**

Seeds laterally and ventrally, in t.s., ellipsoid to ovoid; 1.75–3.50  $\times$  0.65–1.50  $\times$  0.95–2.10 mm long. Hilum linear along the ventral side to the base (Fig. 1Q, 1T). Elaiosome present in all taxa; heart shaped to ovoid with a linear shaped elaiosome attached underneath, along the ventral area. Elaiosome usually white to light brown to brown, membranaceous, caducous. Testa usually shiny or rarely dull; dark brown to rarely black with grey area due to the presence of wax (*Z. veronicea* subsp. *veronicea*). Testa surface pattern Type VI (ridged, the interridge area is formed by both cells that form the ridges and cells that do not form the ridges, and interridge area is variously patterned; Fig. 2T–Y). Testa interridge area variable: colliculate (*Z. arborescens* subsp. *arborescens*; *Z. laevigata* – with wax), concave (*Z. furfuracea* subsp. *euthadenia*), alveolate (*Z. minutiflora* subsp. *minutiflora* – with

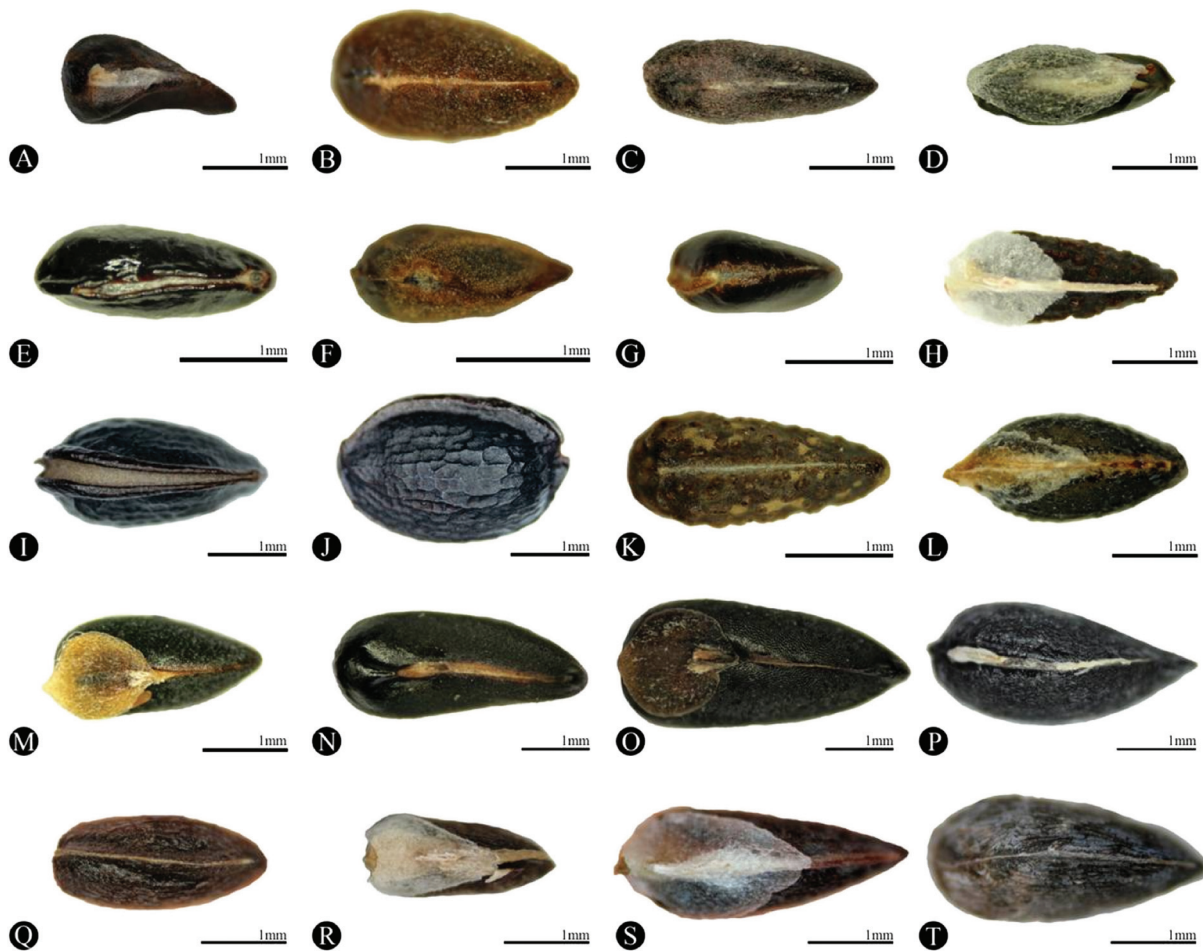


Figure 1. LM micrographs of seeds in *Boronia*, *Boronella*, *Neobyrsesia* and *Zieria*. (A) *Boronella crassifolia*, (B)–(O) *Boronia*, (B) *B. alata*, (C) *B. algida*, (D) *B. gunnii*, (E) *B. pinnata*, (F) *B. scabra* subsp. *scabra*, (G) *B. parviflora*, (H) *B. anethifolia*, (I)–(J) *B. busselliana*, (K) *B. occidentalis*, (L) *B. ramosa* subsp. *anethifolia*, (M) *B. alulata*, (N) *B. odorata*, (O) *B. warrumbunglensis*, (P) *Neobyrsesia suberosa*, (Q)–(T) *Zieria*, (Q) *Z. arborescens* subsp. *arborescens*, (R) *Z. furfuracea* subsp. *euthadenia*, (S) *Z. laevigata*, (T) *Z. veronicea* subsp. *veronicea*. All in ventral view, except (L) in lateral view. The micrographs are arranged in infrageneric order in *Boronia*.

wax), usually flat (colliculate pattern is sometimes found in *Z. smithii* subsp. *smithii*, rarely in *Z. veronicea* subsp. *veronicea* with wax). Testa thickness as follows: exotesta 4.50–68.47  $\mu\text{m}$  thick, mesoteta 44.07–169.38  $\mu\text{m}$  thick, endotesta 3.40–12.17  $\mu\text{m}$  thick (Fig. 4F, Table 6).

–Taxa examined: *Z. arborescens* subsp. *arborescens*, *Z. furfuracea* subsp. *euthadenia*, *Z. laevigata*, *Z. minutiflora* subsp. *minutiflora*, *Z. smithii* subsp. *smithii*, *Z. veronicea* subsp. *veronicea*.

## Discussion

Seed morphological characters of 31 taxa of *Boronia*, *Boronella*, *Neobyrsesia* and *Zieria* were examined. The seeds vary in shape, sizes, hilum and elaiosome characters and testa surface patterns.

Characters of the testa surface pattern, hilum (surrounded by labiose margin or not) and elaiosome shape were important in the studied group. *Boronia* sect's *Alatae* and *Algidae* are each distinguished by testa surface patterns

(Types IV & V; Fig. 5E, Table 4–5) which are considered to be apomorphic characters for these sections. The sectional circumscription of the two sections is supported by seed testa pattern characters.

Section *Boronia* is distinguished by the unique testa surface pattern Type I (Fig. 5E, Table 5) which can be considered to be an apomorphy. *Boronia scabra* subsp. *scabra* is unique in sect. *Boronia* (Fig. 2I, 5E, Table 5) in having testa surface pattern Type IIIa, which may be a reversal. The hilum surrounded by the labiose margin appears to be an apomorphy for *Boronia* ser. *Boronia* (Fig. 1E–1F). This feature is also present in *B. busselliana* (sect. *Cyanothamnus*; Fig. 1I) though this appears to be a parallelism (see below). In sect. *Boronia* ser. *Pedunculatae*, the hilum is not surrounded by the labiose margin (Fig. 1G), and instead it has a basal pulpy raphe and this structure is considered to be an apomorphy for the series (Wilson 1998).

*Boronia* sect. *Cyanothamnus* is characterised by a combination of characters: the testa surface pattern Type IIIa, the testa with hilly protrusions (Fig. 1H, 1K–L, 3C), and the linear hilum to the base (Fig. 1K) that is not surrounded by the labiose margin (except *B. busselliana*; Fig. 1I).

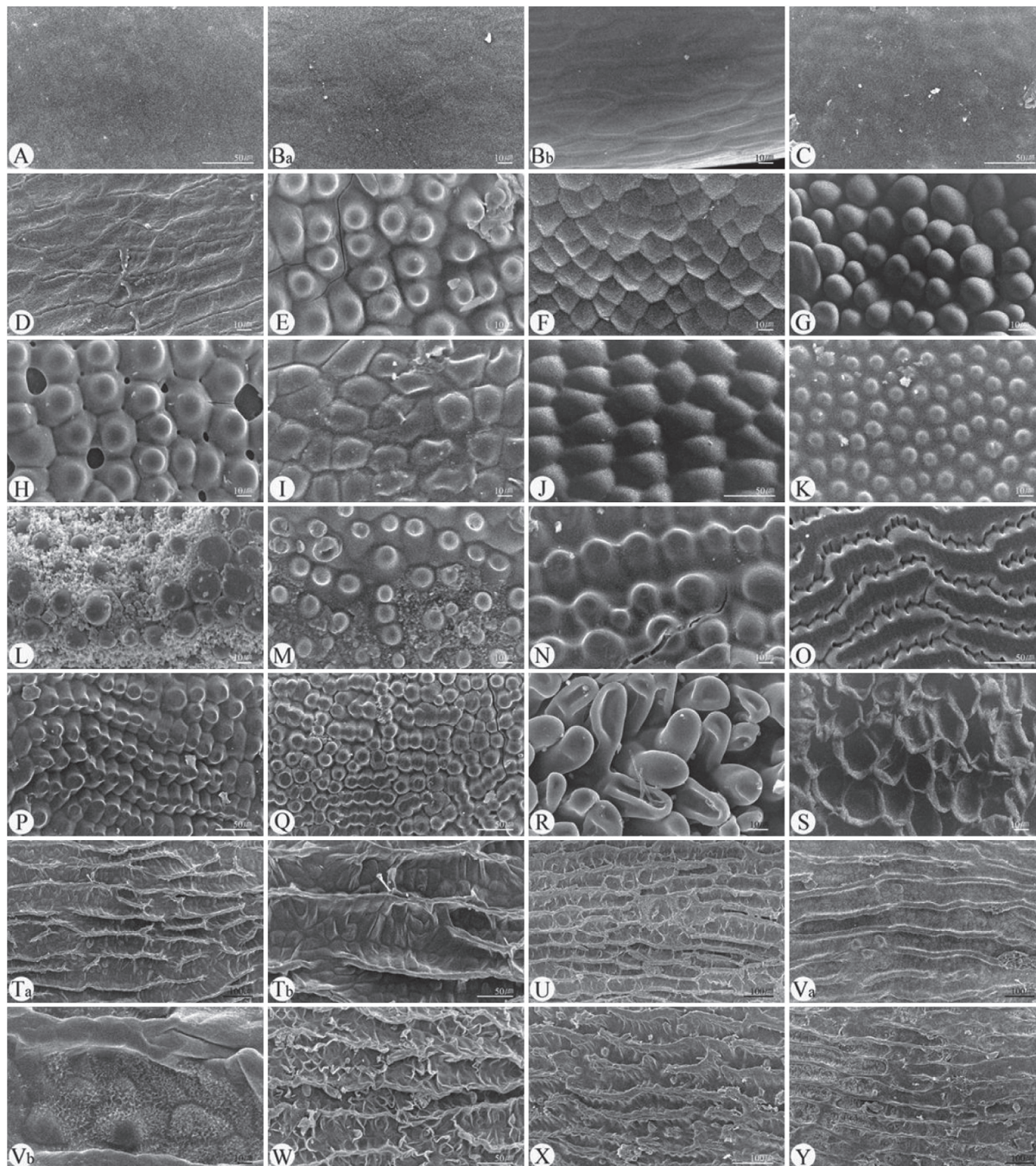


Figure 2. SEM micrographs of seeds in *Boronia*, *Boronella*, *Neobyrsesia* and *Zieria* based on testa surface pattern. (A)–(C) Type I: (A) *Boronia falcifolia*, (Ba)–(Bb) *B. pilosa* subsp. *pilosa*, (C) *B. thujona*, (D) Type II: *Boronella crassifolia*, (E)–(N) Type IIIa: (E) *Boronia alulata*, (F) *B. busselliana*, (G) *B. cymosa*, (H) *B. odorata*, (I) *B. scabra* subsp. *scabra*, (J) *B. warrumbunglensis*, (K) *B. anethifolia*, (L) *B. coeruleascens* subsp. *spinescens*, (M) *B. occidentalis*, (N) *B. ramosa* subsp. *anethifolia*, (O) Type IIIb: *B. grandisepala* subsp. *acanthophida* (P) Type IIIc: *Neobyrsesia suberosa*, (Q) Type IIIId: *Boronia bowmanii*, (R) Type IV: *B. alata*, (S) Type V: *B. algida*, (T)–(Y) Type VI: (Ta)–(Tb) *Zieria arborescens* subsp. *arborescens*, (U) *Z. furfuracea* subsp. *euthadenia*, (Va)–(Vb) *Z. laevigata*, (W) *Z. minutiflora* subsp. *minutiflora*, (X) *Z. smithii* subsp. *smithii*, (Y) *Z. veronicaea* subsp. *veronicaea*.

Interestingly, *B. busselliana* has a hilum surrounded by labiose margins which is found in most species in ser. *Boronia* (Fig. 1E–F; see above). This taxon also has a reticulate testa in contrast with the hilly protrusions seen in other taxa (Fig. 1H, K–L). *Boronia busselliana* is an unusual species with many autapomorphies, including unusual stamens, but otherwise is closely related to *B. tenuis* and *B. defoliata* with

which it shares additional apomorphies (Duretto, unpubl. data). The hilum surrounded by labiose margins would appear to have evolved twice in *Boronia*.

Section *Imbricatae* is characterised by the shiny grey seeds marked with black spots on ridges and testa with hilly protrusions (Wilson 1998). Section *Valvatae* is characterized by a combination of characters: testa surface pattern (Type

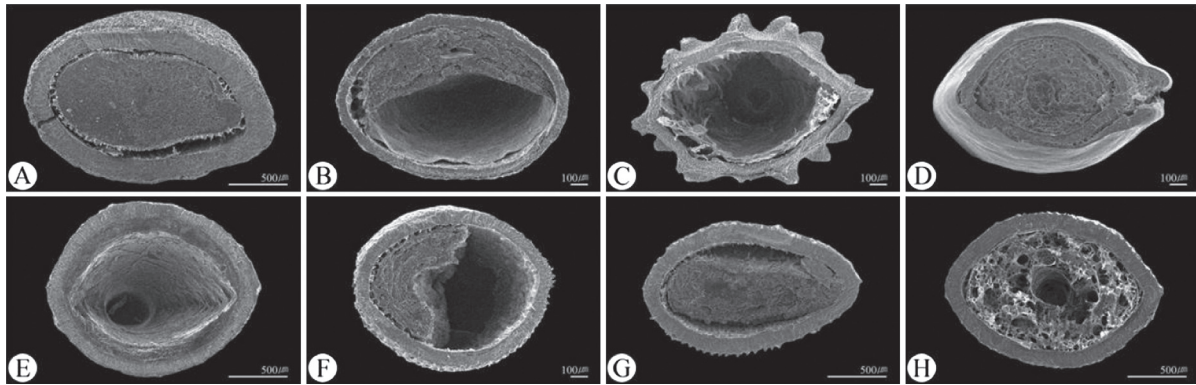


Figure 3. SEM micrographs of seeds in *Boronia*, *Neobyrnnesia* and *Zieria* based on transverse section. (A) *Boronia alata*, (B) *B. algida*, (C) *B. anethifolia*, (D) *B. pinnata*, (E) *Neobyrnnesia suberosa*, (F) *Zieria furfuracea* subsp. *euthadenia*, (G) *Z. laevigata*, (H) *Z. veronica* subsp. *veronica*.

IIIa; Fig. 2E, 2H, 2J) with a few exceptions (Types IIIb, IIIc; Fig. 2O, 2Q), seeds with laterally ovoid and with hilar side flattened shape and the presence of a usually fusiform, thick and persistent elaiosome (Fig. 1M, 1O, Table 5).

Colour, shape, hilum and the testa surface pattern observed in *Boronia* were similar to the previous studies by Wilson (1998), Duretto and Ladiges (1997, 1999) and Duretto (1998, 1999, 2003).

*Boronella* is characterised by a unique testa surface, Type II, which by being smooth, is very similar to that found in sect. *Boronia* (Type I). *Neobyrnnesia* is distinguished by its unique testa surface pattern (Type IIIc). The testa surface pattern confirms that reported by Armstrong and Powell (1980) who described the seed surface pattern as lineolate. Linear ridges constructed of a row of partially fused cells were not found in the other genera. The last genus in this study, *Zieria* has a linear hilum to the base and the testa surface pattern Type VI (Fig. 2T–Y). Powell and Armstrong (1980) divided the testa surface pattern types of 23 species into 40 surface patterns based on structural similarity. Though individually distinct, all the observed species of *Zieria* were

similar, when compared to the other genera, and so were all assigned as having the unique testa surface pattern Type VI. Colliculate pattern (*Z. pilosa*) was also observed in Powell and Armstrong (1980). While the results were mostly consistent with the previous study, often more variation in testa surface patterns were observed or the testa surface pattern observed in this study did not correspond to that observed by Powell and Armstrong (1980). They examined many more specimens per taxon than was done for this study, and the discrepancy may be due to this.

The transverse sectional study of the investigated taxa showed that the thickness of the seed coat layer does not offer useful characters for classification. Mesotesta (sclerenchymatous layer) was the thickest layer in all the studied taxa (Fig. 4, Table 6). However, it is interesting to note that among six taxa studied in *Zieria*, *Z. arborescens* subsp. *arborescens*, *Z. laevigata* and *Z. veronica* subsp. *veronica* have two to three times as thicker mesotesta compared to rest of the studied taxa in *Zieria* (Table 6). According to Auld (2001), in *Z. arborescens* and *Z. laevigata*, heat and fire are related to the seed germination.

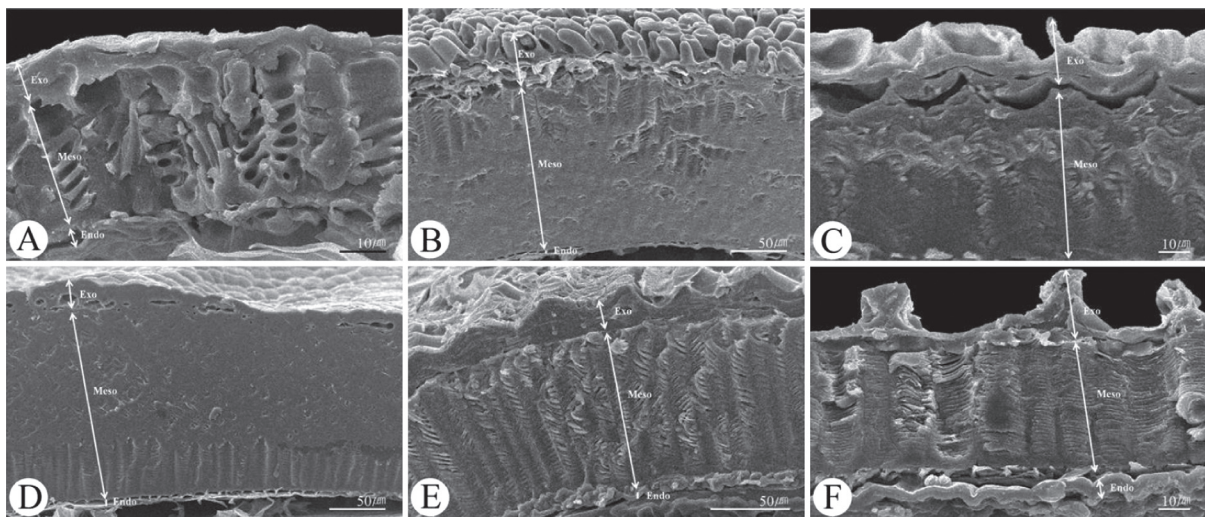


Figure 4. SEM micrographs of enlarged transverse section of seed in *Boronia*, *Boronella*, *Neobyrnnesia* and *Zieria*. (A) *Boronella crassifolia*, (B) *Boronia alata*, (C) *B. algida*, (D) *B. busselliana*, (E) *Neobyrnnesia suberosa*, (F) *Zieria smithii* subsp. *smithii*. Exo: extotesta, meso: mesotesta, endo: endotesta.

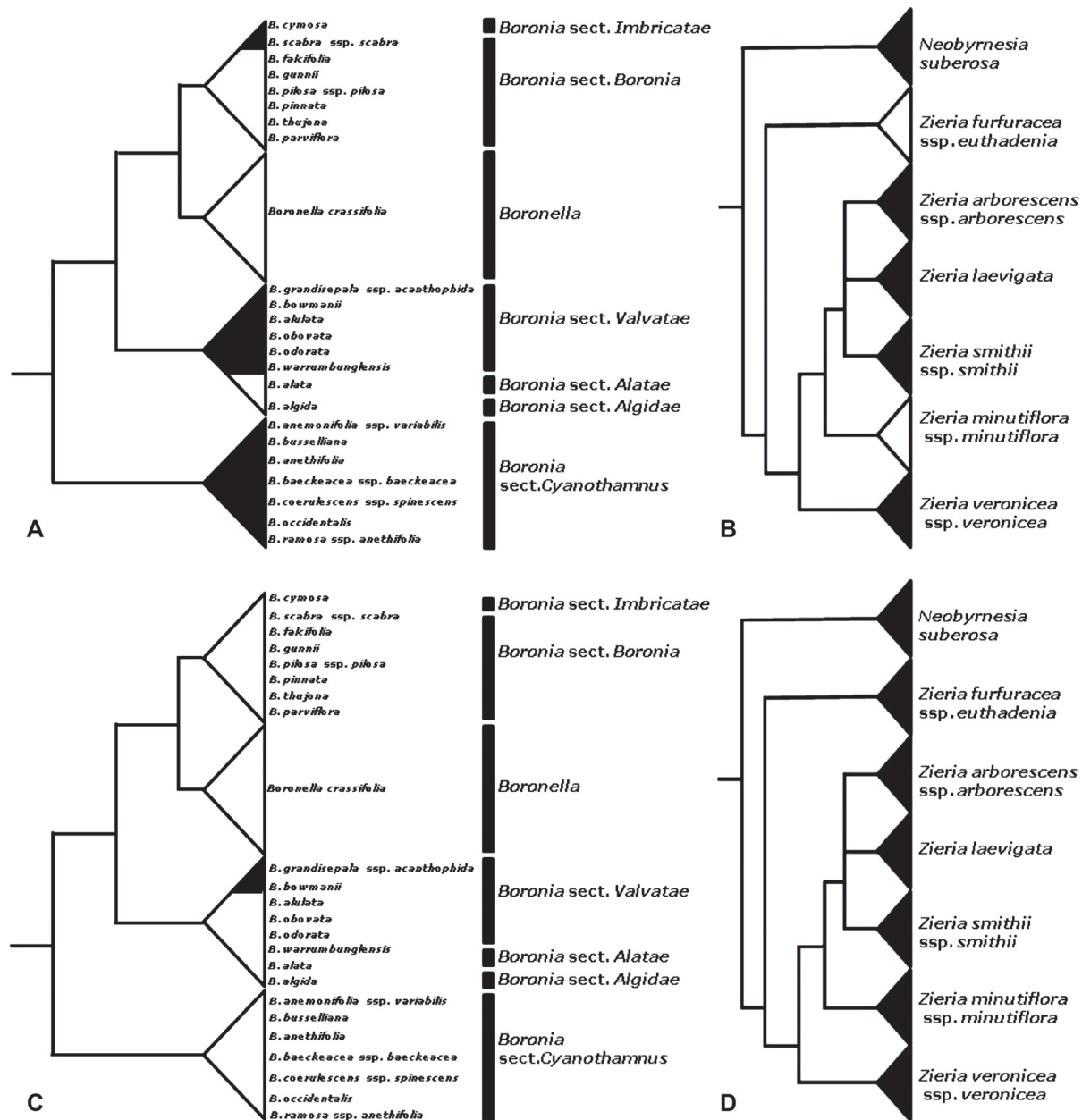


Figure 5. Diagrams of colliculate presence, ridge presence, testa surface patterns in *Boronia*, *Boronella*, *Neobyrnesia* and *Zieria* on most recent cladograms. (A), (C), (E) Simplified tree of *Boronia* and *Boronella* based on Weston et al. 1984, and (B), (D), (F) of *Neobyrnesia* and *Zieria* based on Armstrong 2002. (A)–(B) Colliculate presence (white: absent, black: present), (C)–(D) Ridge presence (white: absent, black: present), (E)–(F) Testa surface pattern types (see Table 4), Type I: vertical lines (▨▨▨▨); Type II: horizontal lines (▤▤▤▤); Type III: four subtypes – Type IIIa: black (■); Type IIIb: diagonal lines from upper right to lower left (▧▧▧▧); Type IIIc: black with white dots (▣▣▣▣); Type IIId: white (□); Type IV: diagonal lines from upper left to lower right (▩▩▩▩); Type V: horizontal and vertical lines (▧▧▧▧); Type VI: grey (■).

Elaiosomes were observed in *Boronella*, *Boronia* (all sections), *Neobyrnesia* and *Zieria* (Fig. 1D, 1H, 1L–M, 1O, 1R–S; Wilson 1998, Duretto 1999, 2003). Some of elaiosomes in *Boronia* and related genera are caducous. In some taxa the absence of elaiosome might be due to this. Thick, persistent and fusiform elaiosomes were observed only in *Boronia* sect. *Valvatae*. Most elaiosomes seen in this study are derived from the placental endocarp and cover the hilum area. The basal pulpy raphe observed in *Boronia* ser. *Pedunculatae* can also be considered to be a type of elaiosome but is not homologous with the elaiosome found on the ventral portion of the seed.

Grob and Grob (2003) stated elaiosomes can originate from various seed tissues (e.g. hilum, raphe) or fruit appendages (e.g. detaching tissues of the fruit, exocarp). Elaiosomes are often closely associated with myrmecochory (i.e. ant dispersal; Sernander 1906, Mark and Olesen 1996). Both *Boronia parviflora* and *B. pinnata*, which were examined in this study, have been reported to be dispersed by ants (Rice and Westoby 1981). The colour of elaiosomes usually attracts specific animal groups, and a white or a yellow elaiosome is usually associated with myrmecochory (Cavanagh 1980). The presence of the elaiosome that is derived from the placental

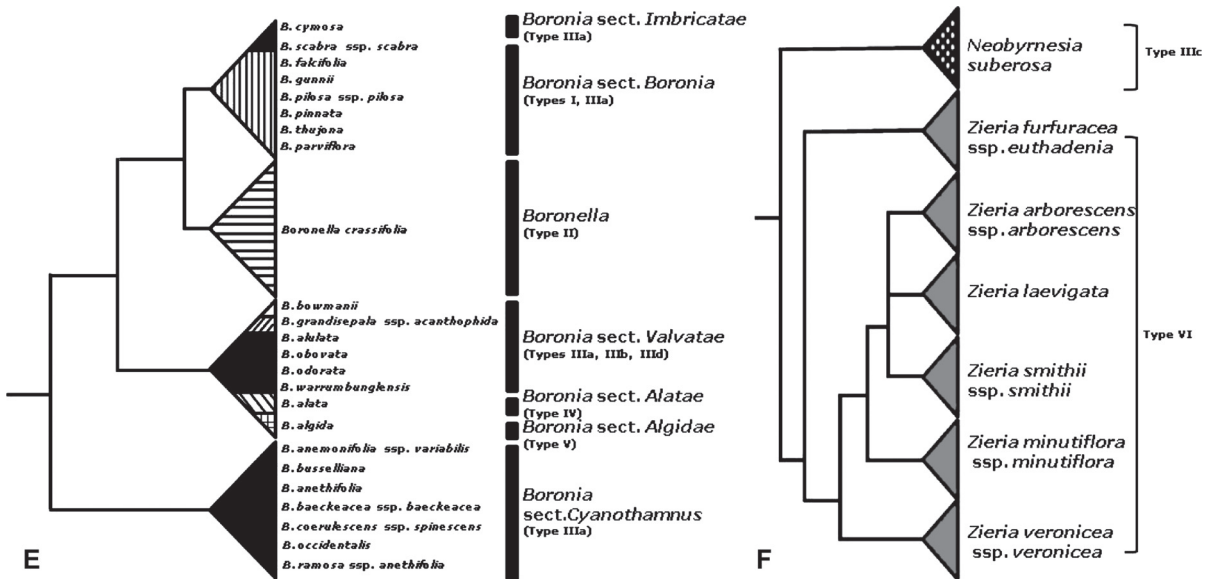


Figure 5. (Continued).

endocarp appears to be an underlying plesiomorphy for *Boronia* and related genera though the one derived from the raphe in ser. *Pedunculatae* is an apomorphy for the series.

## Systematic implications

Cladistic analyses of *Boronia* indicate that all six sections are monophyletic (Weston et al. 1984, Duretto and Ladiges 1999, Duretto 2003), though the position of *Boronella* and the structure of sect. *Boronia* remain unresolved (Weston et al. 1984, M. Bayly and M. Duretto unpubl. data).

In this study, potential apomorphies have been identified for *Boronia* sects. *Alatae* (testa pattern Type IV), *Algidae* (Type V), *Boronia* (Type I, apparently reversed in *B. scabra* subsp. *scabra*), ser. *Boronia* (hilum with labiose margins), ser. *Pedunculatae* (basal pulpy raphe), *Imbricatae* (seed colour), species groups in sect. *Valvatae* (Type IIIb, d, fusiform elaiosome), as well as for *Boronella* (Type II), *Neobyrsesia* (Type IIIc) and *Zieria* (Type VI) (see Table 4, 5).

The general colliculate surface observed in *Boronia* (sects. *Cyanothamnus*, *Imbricatae*, *Valvatae*), *Neobyrsesia* and *Zieria* (Fig. 5A–B) appears to be an underlying plesiomorphic condition, versus a smooth surface as observed in sect. *Boronia* and *Boronella* (Types I, II). The ridges observed in *Neobyrsesia*, *Zieria* and some species in *Boronia* sect. *Valvatae* (Types IIIb–d, VI; Fig. 5C–D) and the unique inter-ridge area seen in *Zieria* (see Table 4) can be considered to be apomorphies.

The colliculate testa surface pattern Type IIIa (Fig. 2I) in *Boronia scabra* subsp. *scabra* is distinctive from that seen in the remainder of ser. *Boronia* (Fig. 2A–Ba, 2C) and may be a reversal. Wilson (1971) placed this species in sect. *Boronia* ser. *Ovatae* (now placed in synonymy under ser. *Boronia*). The taxon has an ellipsoid (short) hilum (Fig. 1F; all linear in ser. *Boronia*, Fig. 1E; Wilson 1971, 1998). To resolve the position of the taxa a more detailed study, such as molecular work, is needed.

The smooth testa (Types I, II) of *Boronia* sect. *Boronia* (Fig. 2A–Ba, 2C) and *Boronella* (Fig. 2D) appears to be a good apomorphy linking these two taxa (though apparently reversed in *Boronia scabra* subsp. *scabra*). These taxa differ in that in the former the cell walls are generally not visible and in *Boronella* the more or less rectangular cells are visible. It is interesting to note that the marginal side of seed of *B. pilosa* subsp. *pilosa* (sect. *Boronia*) has vague *Boronella* like rectangular cells (Fig. 2Bb). *Boronella* and *Boronia* sect. *Boronia* also share the apomorphy of the anther connective is subapical on the filament tip (Weston et al. 1984). Weston et al. (1984) showed that *Boronella* was sister to sect. *Boronia* and recommended that *Boronella* to be included in *Boronia*. The close relationship of sect. *Boronia* and *Boronella* is also supported by recent molecular data (M. Bayly pers. comm.) and further work is required.

The ridged surface patterns of the testa are observed in *Boronia* sect. *Valvatae*, *Neobyrsesia* and *Zieria* (Fig. 5C–D). The ridges seen in *Zieria* are different from those seen in *B. grandisepala* subsp. *acanthophida* (Fig. 2O; see also Duretto and Ladiges 1997), *B. bowmanii* (Fig. 2Q) and *Neobyrsesia* (Fig. 2P) as the interridge area is formed by both cells that form the ridges and cells that do not form the ridges. In *Boronia* sect. *Valvatae* (subsects. *Grandisepalae*, *Bowmaniae*) and *Neobyrsesia*, a row of cells form the linear ridges and the interridge is formed by the sides and bases of the same cells. The ridges of *B. bowmanii* are different from the other taxa as the cells are irregularly fused and the ridges are rare. The ridges seen in *Boronia* subsect. *Grandisepalae* and *Neobyrsesia* are similar in that the ridges are linear. The difference between the two is that the cells on ridges are partially fused in *Neobyrsesia* and completely fused that indistinctive in *Boronia* subsect. *Grandisepalae*. Interestingly, most taxa that have the linear ridges are restricted to a small area on the Arnhem Land Plateau (the Northern Territory; Appendix 1) and also share valvate and persistent petals (Duretto 2008). These characters appear to be a parallelism, and probably are a response and adaptation to similar niches in the dissected

sandstone landscape (Duretto 2008). Recent molecular work indicates that *Neobyrnesia* is more closely related to *Zieria* than it is to *Boronia* (M. Bayly pers. com.). It would appear that the ridges on the testa have evolved independently at least four times in these genera, twice in *Boronia* sect. *Valvatae*, and provide useful taxonomic characters in *Boronia* sect. *Valvatae* (Duretto and Ladiges 1997, 1999, Duretto 1999, 2008), *Neobyrnesia* (Armstrong and Powell 1980) and *Zieria* (Powell and Armstrong 1980, Armstrong 2002).

In conclusion, seed morphological data, especially testa surface patterns, was partially congruent with the current infraspecific classification of *Boronia*, with most sections having apomorphies. It also provides additional support for the placement of *Boronella* near *Boronia* sect. *Boronia*. Further study, such as molecular data, might help clarify the relationship between *Boronia* and *Boronella*. The hilum (surrounded by labiose margins or not) and elaiosome shape also provide useful characters of *Boronia* at infrageneric levels. *Neobyrnesia* and *Zieria* both had unique testa surface patterns. The seed morphological data contribute to our understanding of systematic relationship in the subtribe *Boroniinae*.

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## References

- Armstrong, J. A. 2002. *Zieria* (Rutaceae): a systematic and evolutionary study. – *Austral. Syst. Bot.* 15: 277–463.
- Armstrong, J. A. and Powell, J. M. 1980. *Neobyrnesia* (Rutaceae): a new genus endemic to northern Australia. – *Telopea* 1: 399–408.
- Auld, T. D. 2001. The ecology of the Rutaceae in the Sydney region of south-eastern Australia: poorly known ecology of a neglected family. – *Cunninghamia* 7: 213–239.
- Barthlott, W. 1981. Epidermal and seed surface characters of plants: systematic applicability and some evolutionary aspects. – *Nord. J. Bot.* 1: 345–355.
- Barthlott, W. 1984. Microstructural features of seed surfaces. – In: Heywood, V. H. and Moor, D. M. (eds), *Current concepts in plant taxonomy*. Academic Press, pp. 95–105.
- Benthams, G. 1863. *Flora Australiensis*. I. – Lovell and Co.
- Cavanagh, A. K. 1980. A review of some aspects of the germination in *Acacias*. – *Proc. Roy. Soc. Victoria* 9: 161–180.
- Chase, M. et al. 1999. Phylogenetic relationships of Rutaceae: a cladistic analysis of the subfamilies using evidence from *rbcL* and *atpB* sequence variation. *Amer. J. Bot.* 86: 1191–1199.
- Denk, T. and Oh, I.-C. 2006. Phylogeny of Schisandraceae based on morphological data: evidence from modern plants and fossil record. – *Pl. Syst. Evol.* 256: 113–145.
- Dixon, K. W. et al. 1995. The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. – *Oecologia* 101: 185–192.
- Duretto, M. F. 1997. Taxonomic notes on *Boronia* species of north-western Australia, including a revision of the *Boronialanuginosa* group (*Boronia* section *Valvatae*: Rutaceae). – *Nuytsia* 11: 301–346.
- Duretto, M. F. 1998. *Boronia* sect. *Valvatae* (Benth.) Engl. (Rutaceae) in Queensland, Australia. – *Austrobaileya* 5: 263–198.
- Duretto, M. F. 1999. Systematics of *Boronia* section *Valvatae* sensu lato (Rutaceae). – *Muelleria* 12: 1–131.
- Duretto, M. F. 2003. Notes on *Boronia* (Rutaceae) in eastern and northern Australia. – *Muelleria* 17: 19–135.
- Duretto, M. F. 2008. A reassessment of *Boronia* (Rutaceae) in Northern Territory with a key to species, the description of one new species and the reduction, in synonymy, of another species. – *Beagle* 24: 7–13.
- Duretto, M. F. and Forster, P. I. 2007. A taxonomic revision of the genus *Zieria* Sm. (Rutaceae) in Queensland. – *Austrobaileya* 7: 473–544.
- Duretto, M. F. and Ladiges, P. Y. 1997. Morphological variation within the *Boronia grandisepala* group (Rutaceae) and the description of nine taxa endemic to the Northern Territory, Australia. – *Austral. Syst. Bot.* 10: 249–302.
- Duretto, M. F. and Ladiges, P. Y. 1999. A cladistic analysis of *Boronia* section *Valvatae* (Rutaceae). – *Austral. Syst. Bot.* 11: 635–665.
- Engler, A. 1931. Rutaceae. – In: Engler, A. and Prantl, K. (eds), *Die Natürlichen Pflanzenfamilien*. ed. 2, Teil 19a. Verlag von Wilhelm Engelmann, pp. 187–359.
- Grob, E. and Grob, S. 2003. Seed dispersal by ants in a deciduous forest ecosystem. – *Kluwer Academic Publishers*.
- Groppo, M. et al. 2008. Phylogeny of Rutaceae based on two non-coding regions from cpDNA. – *Amer. J. Bot.* 95: 985–1005.
- Hamilton, K. N. et al. 2008. Morphological characterization of seeds of three Australian wild *Citrus* species (Rutaceae): *Citrus australasica* F. Muell., *C. indora* F. M. Bailey and *C. garrawayi* F. M. Bailey. – *Genet. Resour. Crop Evol.* 55: 683–693.
- Hartley, T. G. 1977. A revision of the genus *Acradenia* (Rutaceae). – *J. Arnold Arbor.* 58: 171–181.
- Hartley, T. G. 1995. A new combination in *Boronella* (Rutaceae) and a view on relationships of the genus. – *Bull. Mus. Natl. Hist. Nat., B, Adansonia (Sér. 4)* 17: 107–111.
- Holmgren, P. K. et al. 1990. *Index herbariorum*, part I. The herbaria of the world, 8th edn. New York Botanical Garden.
- Hong, S.-P. 1993. Reconsideration of the generic status of *Rubrivina* (Polygonaceae, Persicariaceae). *Pl. Syst. Evol.* 186: 95–122.
- Kubitzki, K. et al. 2011. Rutaceae. – In: Kubitzki, K. (ed), *The families and Genera of Vascular plants, X, Flowering Plants, Eudicots – Sapindales, Cucurbitales, Myrtaceae*. Springer-Verlag, pp. 276–356.
- Liu, Y.-P. et al. 1997. Pharmacognostical studies on the Sino-Japanese crude drugs “Huajiao” and “Sansho” (Part 4) determination of botanical origin of Chinese crude drug “Jiaomu” by Scanning Electron Microscopy. – *J. Jpn. Bot.* 72: 93–109.
- Mark, S. and Olesen, J. M. 1996. Importance of elaiosome size to removal of ant-dispersed seeds. – *Oecologia* 107: 95–101.
- Moon, H.-K. and Hong, S.-P. 2006. Nutlet morphology and anatomy of the genus (Lamiaceae: Mentheae). – *J. Plant Res.* 119: 633–644.
- Powell, J. M. and Armstrong, J. A. 1980. Seed surface structure in the genus *Zieria* Sm. (Rutaceae). – *Telopea* 2: 85–112.
- Rice, B. and Westoby, M. 1981. Myrmecochory in sclerophyll vegetation of the West Head, New South Wales. – *Austral. J. Ecol.* 6: 291–298.
- Roche, S. et al. 1997. Seed ageing and smoke: partner cues in the amelioration of seed dormancy in selected Australian native species. – *Aust. J. Bot.* 45: 783–815.

- Schols, P. et al. 2002. Carnoy: a new digital measurement tool for palynology. – *Grana* 41: 124–126.
- Sernander, R. 1906. Entwurf einer Monographie der europäischen Myrmekochoren. – Almqvist and Wiksells.
- Vural, C. et al. 2008. Seed morphology and its systematic implications for genus *Astragalus* L. sections *Onobrychoidei* DC., *Uliginosi* Gray and *Ornithopodium* Bunge (Fabaceae). – *Pl. Syst. Evol.* 274: 255–263.
- Werker, E. 1997. Seed Anatomy. – Gebrüder Borntraeger.
- Weston, P. H. et al. 1984. A cladistic analysis of *Boronia* Sm. and *Boronella* Baill. (Rutaceae). – *Austral. J. Bot.* 32: 187–203.
- Wilson, P. G. 1971. Taxonomic notes on the family Rutaceae, principally of Western Australia. – *Nuytsia* 1: 197–207.
- Wilson, P. G. 1998. New names and new taxa in the genus *Boronia* (Rutaceae) from Western Australia, with notes on seed characters. – *Nuytsia* 12: 119–154.



## Appendix

### Appendix 1. Specimens examined.

Taxon	Distribution	Voucher information
<i>Boronia</i> Sm.		
sect. <i>Alatae</i> Duretto		
<i>B. alata</i> Sm.	W	Australia, SW Western Australia, 16. Nov. 1950. Willis s.n. (MEL)
sect. <i>Algidae</i> Duretto		
<i>B. algida</i> F. Muell.	NS, V	Australia, Victoria, 26. Jan. 1967. Beauglehole ABC 22523 (MEL)
sect. <i>Boronia</i>		
ser. <i>Boronia</i>		
<i>B. falcifolia</i> A. Cunn. ex Endl.	NS, Q	Australia, New South Wales, 24. Oct. 1995. Duretto et al. 665 (BRI)
<i>B. gunnii</i> Hook. f.	T	Australia, Tasmania, 23. Dec. 2003. Duretto and Baker 1650 (MEL)
<i>B. pilosa</i> Labill. ssp. <i>pilosa</i>	T, V	Australia, Tasmania, 13. Jan. 1996. Duretto 859 (HO)
<i>B. pinnata</i> Sm.	NS	Australia, New South Wales, 29. Oct. 1995. Duretto et al. 697 (BRI)
<i>B. scabra</i> Lindl. ssp. <i>scabra</i>	W	Australia, Western Australia, 30. Oct. 1998. Weston 2185 (MEL)
<i>B. thujona</i> A. R. Penfold & M. B. Welch	NS	Australia, New South Wales, 29. Oct. 1995. Duretto et al. 696 (BRI)
ser. <i>Pedunculatae</i>		
<i>B. parviflora</i> Sm.	NS, Q, S, T, V	Australia, Tasmania, 19. Dec. 2008. Wood and Lang 67 (HO)
sect. <i>Cyanothamnus</i> (Lindl.) F. Muell.		
<i>B. anemonifolia</i> A. Cunn. ssp. <i>variabilis</i> (Hook.) P. G. Neish	NS, Q, T, V	Australia, Tasmania, 6. Jan. 1996. Neish et al. 54 (HO)
<i>B. anethifolia</i> A. Cunn. ex Endl.	NS, Q	Australia, New South Wales, 25. Oct. 1995. Duretto et al. 676 (BRI)
<i>B. baeckeacea</i> F. Muell. ssp. <i>baeckeacea</i>	W	Australia, Western Australia, 12. Sep. 1964. Wilson 3068 (MEL)
<i>B. busselliana</i> F. Muell.	W	Australia, Western Australia, ca. Feb. 1980. Chapman s.n. (CANB)
<i>B. coerulescens</i> F. Muell. ssp. <i>spinescens</i> (Benth.) Paul G. Wilson	W	Australia, Western Australia, 4. Oct. 1961. Willis s.n. (MEL )
<i>B. occidentalis</i> Duretto	NS, Q	Australia, New South Wales, without date, Jobson1883 (MEL)
<i>B. ramosa</i> (Lindl.) Benth. ssp. <i>anethifolia</i> (Bartl.) Paul G. Wilson	W	Australia, SW Western Australia, without date, Archer 166 (MEL)
sect. <i>Imbricatae</i> Engl.		
<i>B. cymosa</i> Endl.	W	Australia, Western Australia, 11. May. 1990. Smith 1284 (MEL)
sect. <i>Valvatae</i> (Benth.) Engl.		
<i>B. alulata</i> Benth.	Q	Australia, Queensland, 15. Jun. 2007. Forster and Mcdonald 32652 (HO)
<i>B. bowmanii</i> F. Muell.	NS, Q	Australia, Queensland, 04. Mar. 1992. Clarkson and Neldner 9330 (BRI)
<i>B. grandisepala</i> F. Muell. ssp. <i>acanthophida</i> Duretto	NT	Australia, Northern Territory, 28. Mar. 1984. Craven and Wightman 8307 (HO)
<i>B. obovata</i> C. T. White	Q	Australia, Queensland, 09. Sep. 1992. Duretto and Bayly 302 (BRI)
<i>B. odorata</i> Duretto	Q	Australia, Queensland, 07. Sep. 1992. Duretto 280 (BRI)
<i>B. warrumbunglensis</i> P. H. Weston	NS	Australia, New South Wales, 27. Dec. 1997. Duretto and Jenz 73 (MEL)
<i>Boronella</i>		
<i>B. crassifolia</i> Guillaumin	N	New Caledonia, Taom, Oct. 1969. Mackee 20969 (NOU)
<i>Neobyrnnesia</i>		
<i>N. suberosa</i> J. A. Armstr.	NT	Australia, 30. Mar. 1981. Craven 6625 (CANB)
<i>Zieria</i> Sm.		
<i>Z. arborescens</i> Sims ssp. <i>arborescens</i>	NS, Q, T, V	Australia, Tasmania, 10. Jan. 1984. Buchanan 2385 (HO)
<i>Z. furfuracea</i> R. Br. ex Benth. ssp. <i> euthadenia</i> J. A. Armstr.	NS, Q	Australia, Queensland, 9. Aug. 1996. Forster and Leiper PIF 19503 (MEL)
<i>Z. laevigata</i> Bonpl.	NS, Q, V	Australia, New South Wales, 4. Nov. 1979. Rees 165 (MEL)
<i>Z. minutiflora</i> Domin ssp. <i>minutiflora</i>	NS, Q	Australia, Queensland, 11. Sep. 2002. Forster PIF28821 (MEL)
<i>Z. smithii</i> Jacks. var. <i>smithii</i>	NS	Australia, Victoria, 20. Oct. 1991. Ross and Coles 3458 (HO)
<i>Z. veronicea</i> (F. Muell.) Benth. ssp. <i>veronicea</i>	S, T, V	Australia, Tasmania, 19. Dec. 2008. Lang and Lang 68 (HO)

N: New Caledonia, NS: New South Wales, NT: Northern Territory, Q: Queensland, S: Southern Australia, T: Tasmania, V: Victoria, W: Western Australia.