New species and a new hybrid in the *Viola hederacea* species complex, with notes on *Viola hederacea* Labill.

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Abstract

The *Viola hederacea* Labill. species complex is widespread in south-eastern Australia. It has often been considered problematic, with numerous forms difficult to adequately diagnose and distinguish. This paper results from an assessment of the complex based on extensive field observations, which have shown that the complex is tractable and comprises a number of morphologically and ecologically distinct species. Two new species, *Viola banksii* K.R. Thiele & Prober *sp. nov.*, and *V. eminens* K.R. Thiele & Prober *sp. nov.*, and a new hybrid, *V. ×zophodes* K.R. Thiele & Prober *nothosp. nov.*, are described and illustrated, and a new circumscription provided for *Viola hederacea sens. str.*

Introduction

The *Viola hederacea* Labill. species complex comprises all taxa in *Viola* Section *Erpetion* (Sweet) Becker, characterised by non-leafy stipules and flowers that are saccate rather than spurred on the anterior petal. Apart from a single doubtful collection from Malaya (Moore 1962), the complex is restricted to Australia, where it has a wide distribution from south-eastern South Australia, through southern Victoria, Tasmania, and eastern New South Wales to Queensland north as far as Atherton (Fig. 1; Adams 1982; Seppelt 1986; James 1990; Entwisle 1996). Many forms are recognisable over this range.

Adams (1982), in the most recent treatment of the complex, described a number of subspecies of *V. hederacea*. Two of these have since been raised to species rank as *V. cleistogamoides* (L.G. Adams) Seppelt and *V. fuscoviolacea* (L.G. Adams) T.A. James. *Viola sieberiana* Spreng., reduced by Adams (1982) and others to a subspecies of *V. hederacea*, has since been reinstated by most authors (e.g. Seppelt 1986; James 1990; Entwisle 1996), while *V. hederacea* subsp. *seppeltiana* L.G. Adams has been rejected as distinct from *V. sieberiana* by Seppelt (1986). The subspecies *V. hederacea* subsp. *perreniformis* L.G. Adams and *V. hederacea* subsp. *curtisiae* L.G. Adams still stand.

Even with these taxa removed, the residual nominal form is still highly variable and problematic. Seppelt (1986), treating the complex in South Australia, noted a 'perplexing array of leaf forms', but considered that 'there is little variation in floral morphology'. James (1990), treating the complex for the *Flora of New South Wales*, described seven 'forms' of *V. hederacea*, based primarily on leaf shapes assessed from herbarium specimens, but regarded that formal recognition of these was premature. Entwisle (1996) remarked that 'there is a need for Australia-wide studies to clarify species concepts and appropriate nomenclature'.

The present paper results from an ongoing study of the *V. hederacea sens. lat.* complex. By contrast with most earlier work, which has been largely herbarium-based, our study has focused on field observation of living material and ecological characteristics from throughout the geographic range of the complex. These have shown that the *Viola hederacea* species complex is tractable, and that it comprises a number of discrete and easily recognisable taxa differing in floral, vegetative and ecological characters. Importantly, almost throughout its range are found areas where two or more distinct taxa grow together or in close proximity, usually with little or no evidence of

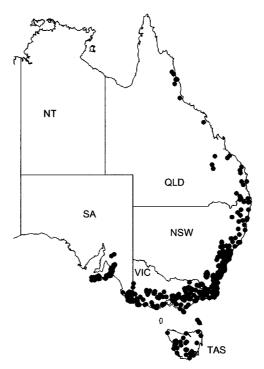


Figure 1. Distribution of the *Viola hederacea* species complex in Australia (based on specimen data from AD, BRI, CANB, MEL, NSW)

hybridisation or introgression and with discrete morphological and ecological differences. Results from the field study have subsequently allowed a more careful appraisal of herbarium material, which has confirmed the distinctness of these taxa over wide geographic ranges.

In this paper we describe and discuss *V. hederacea* Labill. *sens. str.*, *V. banksii* K.R. Thiele & Prober *sp. nov.*, *V. eminens* K.R. Thiele & Prober *sp. nov.* and *V. x. zophodes* K.R. Thiele & Prober *nothosp. nov.* Other taxa will be dealt with in subsequent papers.

Characters in the Viola hederacea species complex

All members of the *Viola hederacea* species complex are stoloniferous perennial herbs, often forming large, clonal colonies. Leaves are mostly borne in false whorls on contracted stems at ground level, but in some taxa the stems may become elongated with caulescent, alternate leaves, particularly when the plants are growing amongst shrubs or other dense vegetation. In some taxa (particularly *V. sieberiana*), the contracted stems are woody and densely covered with old leaf bases and stipules, while in others they are fleshier and more or less naked.

Leaves are petiolate, with a flat, irregularly toothed blade. The shape of the blade is variable, even within a single clonal colony. Leaf shape is a useful diagnostic feature for taxa, but with the limitation that exposed leaves are smaller and less distinctive than leaves from lush growth in sheltered sites. Some taxa, such as *V. fuscoviolacea*, *V. cleistogamoides* and *V. sieberiana* tend to have ovate-rhomboid leaves with a cuneate base, while other taxa tend towards reniform leaves with a broad to narrow basal sinus. Because of the variability of leaves within taxa and individuals, these differences cannot be used consistently to discriminate taxa. Herbarium specimens of *Viola* usually have an inadequate selection of well-developed leaves.

Leaves, petioles and stems may be glabrous or bear sparse, short, unicellular hairs. Degree of pubescence with such hairs is variable, and appears to be of limited taxonomic value.

Flowers are borne singly on short or long, unbranched scapes, each scape bearing a pair of stipule-like bracteoles usually near its middle; the scape is usually slightly geniculate at the bracteoles. Flowers in *V. cleistogamoides* and *V. fuscoviolacea* are characteristically borne on scapes distinctly shorter than the leaves, while in all other taxa the flowers are borne above or well above the level of the leaves.

Flowers are zygomorphic and personate. The calyx comprises five free sepals, and is green or (in some taxa) flushed purple. The corolla comprises five free petals, scarcely exceeding the sepals in *V. cleistogamoides* and *V. fuscoviolacea*, distinctly exceeding the sepals in all other taxa.

In some taxa the flowers are nearly or quite concolorous white, pale blue, pale violet or (in *V. fuscoviolacea*) blackish-violet, while in others they are strongly discolorous violet-and-white or dark violet on a paler violet ground. Among the discolorous taxa some have sharply demarcated boundaries between the violet and white, while others are more graduated, giving a 'washed out' appearance. The brightness and hue of the violet colour differs between taxa. While there is some variation in colour within taxa, the colours and colour patterns are useful diagnostic features, at least on fresh flowers.

The anterior petal (the lowermost with the flower in its natural position) has a slightly saccate base in the position of the spur in other species of *Viola*. The shape, colouration and venation of this petal is an important diagnostic feature.

The lateral petals are twisted in most species (scarcely so in *V. cleistogamoides* and *V. fuscoviolacea*). The degree of twisting of the lateral petals varies between taxa, and is sometimes a useful taxonomic feature. In most species the adaxial surface of the lateral petals is bearded with white or coloured hairs, varying from a few scattered hairs (in e.g. *V. fuscoviolacea*) to a large, dense patch. The hairs are thickened and sometimes slightly club-shaped. Although the presence or absence of bearded lateral petals has been used as a taxonomic feature (e.g. Adams, 1982) it appears to be of limited value, and occasional clones of all taxa are beardless. When present, however, the extent of the beard may be a useful character.

The posterior petals (the uppermost with the flower in its natural position) are generally obovate, reflexed and clawed, but may vary greatly in shape between clones within one taxon. They are of limited taxonomic value.

The androecium comprises five free stamens, connivent around and obscuring the ovary. Each stamen comprises a short, broad filament and a flattened, introrse anther with a terminal, flattened appendage. The connective between the anther cells may be cream or suffused or blotched with purple. The two anthers adjacent to the anterior petal each bear an abaxial nectariferous gland on the connective between the anther cells. The shape, colour and surface texture of this gland is a useful diagnostic feature.

Pollen in some taxa is cream or white, while in others it is yellow to golden. The taxa with yellow pollen also have a yellow colouration on the inner surfaces of the pollen sacs (at least in fresh material).

The gynoecium comprises three fused carpels forming a unilocular ovary with parietal placentas, surmounted by a simple, geniculate style. The ovary varies from greenish-white, sometimes flushed or flecked with violet, to uniformly dark violet. While ovary colour is variable within all taxa, it may have some limited diagnostic value (e.g. the dark-flowered *V. fuscoviolacea* appears to consistently have pale greenish-white ovaries without any purple flushing).

The fruit is a 3-valved capsule opening +/- explosively on maturity to scatter the globose seeds. Freshly exposed seeds may vary in colour, even within a single capsule, from white to dark purplish-black. Colour of the mature, dried seeds is a valuable diagnostic feature, being dull, pale brown or fawn in some taxa and glossy black in others.



Figure 2. Viola hederacea. a Habit x1; b Flower x2 (K.R. Thiele 2542, CANB).

Taxonomy

1. Viola hederacea Labill., Nov. Holl. Pl. Spec. 1: 66, t. 91 (1805).

Erpetion hederaceum (Labill.) G.Don, Gen. Hist. 1: 335 (1831); Viola hederacea var. genuina Domin, Biblioth. Bot. 89: 427 (1928). Type: 'In capite Van-Diemen', J.Labillardiere: F, n.v.; photo: CANB!

Perennial herb spreading widely by stolons; rootstock sometimes somewhat swollen and bulbous at the stem bases. Stems contracted so that the leaves form rosettes, never elongate with caulescent leaves. Leaves broad-reniform or semi-circular, the largest (4-)15-20(-30) mm long, (5-)20-30(-50) mm wide, 1-1.5(-2) times wider than long, usually truncate at base or occasionally with a broad sinus or broadly cuneate; lamina with 8-16 obscure teeth, glabrous or with scattered unicellular hairs on the upper surface, dark green above, dull greyish-green beneath; petioles (1–)2–8(–12) cm long; stipules narrowly triangular, usually with several small, glandular teeth on each side. Flowers on scapes slightly longer to four times as long as the leaves, usually discolorous violet-and-white (occasionally concolorous pale violet or almost white), the colours usually not strongly demarcated; anterior petal (4-)8-10(-12) mm long, (3-)5-7(-9) mm wide, narrowly- to broadly obovate or cuneate, broadest in the distal third, usually emarginate, with a small green U-shaped blotch at the base, then usually pale to bright violet for over half its length grading to a white apex, with three to many nerves, the midnerve usually not distinct from the lateral nerves and often anastomosing with them; lateral petals spreading, (4–)8–10(–13) mm long, twisted usually to c. 90° (sometimes to 180°), violet at the base grading to white distally; beard covering half or less of the width of the lateral petals, occasionally absent; dorsal petals (4-)8-12(-13) mm long, (2-)4-6(-8) mm wide, obovate to broadly obovate (rarely narrowly obovate), erect to strongly reflexed, usually violet at the flexure grading to white for most of their length. Anthers 1.3-4.0 mm long, cream, often flushed or flecked with violet, the terminal appendages straw-coloured, with short, irregular hairs on the outer margins of the anther cells; anther glands purplish or dull green, shorter than the anther cells, irregularly rugose, broad at the base and each distinctly flattened or depressed towards the other; pollen and interior margins of the anther cells white to cream. Ovary and fruit whitish or pale green, often flecked or flushed purple; style distinctly geniculate at its insertion on the ovary. Seeds 1.2-2.0 mm long, dull, mottled cream and brown (occasionally uniformly reddish-brown), +/- smooth. Fig. 2.

Distribution and habitat. Viola hederacea is common and widespread in south-eastern Australia, from the Mount Lofty Ranges and south-eastern South Australia, throughout Tasmania and southern Victoria, and in eastern New South Wales north to the Northern Tablelands (Fig. 7a). It is typically found on relatively dry soils in forested habitats and on well-drained roadside banks.

In South Australia it is widespread in the South-East region, but is highly localised in the Adelaide Hills, apparently occurring only in the area around Mount Lofty, Belair National Park and near Crafers. Elsewhere on Fleurieu Peninsula and in the Southern Lofty region it is replaced by *V. eminens* (see below). In Victoria it is the most widespread species, occurring commonly in dry to moist forests from the far south-west around Glenelg River and the Grampians Ranges, through the Otway Ranges and thence on both north and south falls of the Great Dividing Range from Melbourne to the New South Wales border. It is replaced on the higher parts of the Great Dividing Range (e.g. summits of Lake Mountain and Mount Baw Baw and on the Errinundra Plateau) by *V. eminens* (see below). *Viola hederacea* is common and widespread throughout much of Tasmania.

In New South Wales *V. hederacea* is the most common species in forests on the eastern part of the Great Dividing Range from the Victorian border to the Blue Mountains and Royal National Park near Sydney. A disjunct but morphologically typical population occurs in the Brindabella Ranges west of Canberra. In northern New South Wales it appears to become patchy and localised, with few collections from widely scattered sites (e.g. Barrington Tops, Glen Elgin). In the Sydney region it is common on shale-derived

soils but is rare on sandstones, where it is replaced by *V. sieberiana* and other as yet undescribed species from the complex. In coastal sites from Ulladulla to the Queensland border it is largely replaced by *V. banksii* (see below).

In the Border Ranges of far northern New South Wales and in Queensland *Viola hederacea* as circumscribed here is replaced by *V. hederacea* subsp. *perreniformis*, a distinct taxon that may be referred to a separate species in a later paper. Note that the description of *V. hederacea* above does not include subsp. *perreniformis*.

Distinguishing features and variation. Viola hederacea sens. str. may be distinguished (Table 1; Fig. 3) from all other taxa in the complex by its obovate to cuneate anterior petals with somewhat irregular venation, usually paler, less sharply discolorous flowers (the violet colouration on the petals grades +/- diffusely into the white rather than being sharply distinct), and reniform or semicircular leaves that are about as broad as long and somewhat discolorous (dark green above, dull greyish-green beneath). Leaf colouration is often a useful though subtle feature on herbarium specimens, dried leaves in V. hederacea being characteristically duller and thicker-textured than the other species in the complex. When fresh flowers are available, V. hederacea appears to be the only species in the complex in which the anther glands are often (although not invariably) purplish.

Seeds of *V. hederacea* differ from all other taxa currently examined (*V. eminens, V. banksii, V. fuscoviolacea, V. cleistogamoides*) with the exception of *V. hederacea* subsp. *perreniformis* in being dull brown (often mottled with pale cream) rather than glossy purplish-black. These seed colours only develop on fully matured seed.

Some collections provisionally referred here to *V. hederacea* have very small flowers (petals 3–5 mm long) that are often almost white and with little or no beard on the lateral petals. These usually grow in very shaded, dry or otherwise unfavourable sites adjacent to more typical *V. hederacea*, with intergrading forms, and occur throughout the range of that species. Such collections have sometimes previously been ascribed to *V. hederacea-V. sieberiana* hybrids (e.g. James 1990), but there is no reason to suspect that hybridisation is occurring between those species. These small-flowered forms warrant further investigation.

	V. hederacea	V. banksii	V. eminens	V. x zophodes
Habitat	Moderately dry to moist sites (not swamps), particularly forest habitats	Coastal headlands, lowland swamps and rainforest or moist sclerophyll forest margins	Moist sites; swamps at lower altitudes, wet sclerophyll forest to snow gum woodlands at high altitudes	Moist sites in high altitude swamps
Typical leaf shape	Reniform to semicircular	Orbicular, with deep sinus	Broad- reniform	Broad- reniform
Flower colour	Weakly to strongly discolorous bright to pale violet with white or pale violet tips, occasionally +/- concolorous	Strongly discolorous, bright violet with prominent white tips	Strongly (rarely weakly) discolorous bright violet with prominent white (occasionally pale violet) tips	Strongly discolorous, dark violet with obscure white tips, occasionally +/- concolorous dark violet
Anterior petal shape	Obovate	Elliptic to circular	Ovate	Ovate
Anterior petal venation	Obscurely triplinerved, the central nerves anastomosing	Distinctly triplinerved, central nerves scarcely anastomosing	Distinctly triplinerved, central nerves scarcely anastomosing	Distinctly triplinerved, central nerves scarcely anastomosing
Lateral petals	Twisted through c. 90°	Twisted through c. 180°	Twisted through c. 180°	Twisted through c. 180°
Beard on lateral petals	≤1/2 width, sometimes absent	>1/2 width	>1/2 width	≥1/2 width
Anther glands	Short, rugose, flattened, often purple	Long, smooth, narrow and high, scarcely flattened, pale green to whitish	Long, smooth, narrow and high, sometimes slightly flattened, pale green to whitish	Short to long, smooth, flattened, pale green to whitish
Pollen colour	White	Golden	Golden	White to pale yellow (sterile)
Mature seed colour	Dull mottled brown and cream	Glossy purple-black	Glossy purple-black	(no seeds set)

Table 1. Diagnostic features of taxa described and discussed in this paper

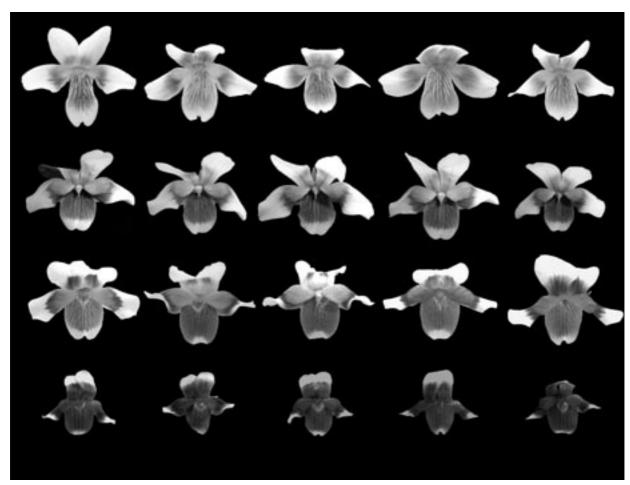


Figure 3. Representative flowers of *V. hederacea* (top row), *V. banksii* (second row), *V. eminens* (third row) and *V. x. zophodes* (bottom row). Approximately natural size.

Notes. The type of *V. hederacea* is from southern Tasmania, collected at Recherche Bay by J.J.H.Labillardiere in 1792. Colour transparencies of the type held at CANB show the typical features for the species, and the illustration accompanying the original description shows well the obovate anterior petals and semicircular leaves that distinguish *V. hederacea* from other taxa in the complex. It is probably the only form occurring in lowland, near-coastal sites in southern Tasmania where Labillardiere would have collected.

Viola hederacea var. elatines D.C. was listed as a synonym of V. hederacea by Adams (1982). Examination of microfiche photographs of the type material indicate that this variety is a synonym of V. banksii (see below).

Selected specimens examined. SOUTH AUSTRALIA: Stirling West, 21 Nov 1958, E.H. Ising s.n. (AD 95904073); Mount Lofty, Oct. 1917, E.H. Ising s.n. (AD 966160089); Mount Lofty Botanic Garden, 12 Jan 1984, B.R. Moore 67 (AD 98943158); Belair National Park, 2 Nov. 1935, E.H. Ising s.n. (AD 98122154); Carpenter Rocks, 5 Nov. 1977, A.G. Spooner 5490 (AD 97813546); Mount Burr Forest, 12 Sept. 1984, C. O'Malley 56 (AD 98615266); 2 km N of Donovan's Landing, near Glenelg River, 4 Nov. 1981, A.A. Munir 5410 (AD 98153296; CANB 350238). Tasmania: 3–4 miles from Cradle Mountain on road to Wilmot, 12 Nov. 1965, M.E. Phillips s.n. (CBG 14363); 7 miles from Lunawanna, South Bruny Island, towards Cape Bruny, 10 Nov. 1965, M.E. Phillips s.n. (CBG 14685); Frenchman's Cap track, at Franklin River, 31 Jan 1969, E.M. Canning s.n. (CBG

27186); Russell Falls, Mount Field National Park, 6 Dec. 1977, L.G. Adams 3364 (CANB 272708); Navarre Plain, 7 km SW of Derwent Bridge on Lyell Highway, 28 Jan 1983, J.G. West 1983 (CANB 402767); Razorback Mine, Dundas, c. 9 km E of Zeehan, 7 Dec. 1977, L.G. Adams 3381 (CANB 272716); Lawson Range, 25 Jan 1986, A. Moscal 11966 (HO 402119; CANB 478725); North Pats River, Flinders Island, 28 Nov. 1976, J.S. Whinray 2280 (CANB 482308). VICTORIA: Mount Buangor, 18 Dec. 1984, A.C. Beauglehole 61360 (MEL 2110520); Glenelg River Road, 11 km W of Halls Gap, Grampians Ranges, 4 Oct 1987, P.C. Jobson 121 (MEL 1561933); About 2.6 miles from Stanley towards Hillsborough, in the Stanley Forest, 19 Oct. 1967, E.M. Canning s.n. (CBG 21375); Otway Ranges, about 4 km N of Beech Forest on the Beech Forest to Gellibrand road, 12 Nov 1960, H.I. Aston s.n. (MEL 594189); 8 km SE of Lang Lang, 19 Oct 1978, T.B. Muir 6206 (MEL 577686); 0.3 miles from Granja Gap towards Tallangatta, 28 Oct 1967, L. Dunn s.n. (CBG 21377); Lilly Pilly Gully, Wilson's Promontory, 21 Nov. 1961, M.E. Phillips s.n. (CBG 2112); Omeo-Corryong road, 2.7 road miles S of Sassafras Gap, 25 Nov 1964, J. Ackland 188 (MEL 1513775); Quarry Road, Briagolong, 29 Nov 1981, R.A. Kilgour 136 (MEL 600007); Thompson River Natural Feature Zone, 6 km SE of Walhalla, 22 April 1985, A.C. Beauglehole 79184 (MEL 677034). New South Wales and ACT: Tantawangalo State Forest, 12 km S of Tantawangalo, 24 April 1993, I.Crawford 2260 (CBG 9317573); "Ngarago", 24.5 km ESE of Nimmitabel, 18 Nov. 1984, J.G. West 4957 (CANB 454245); 4 km past trig on Merricumbene Fire Trail, Deua National Park, 12 Oct. 1993, T.R. Lally 155 (CANB 462632); Below Lee's Spring near Blundell's Valley, Brindabella Range, 20 Nov. 1956, Hj. Eichler 13300 (CANB 389661; AD95814019); Near the start of the walking track from Saltwater Creek to Bittangabee Bay, south of Eden, 15 Sept. 1984, D.E. Albrecht 698 (CANB 357541); Mt. Dromedary, 25 Jan. 1970, N.T. Burbidge 7824 (CANB 236770); Claymore Creek aqueduct offshoot, Watson's Crags Spur, Snowy Mountains, 28 Nov. 1970, J.I. Raine ANU10317 (CANB 247164); 6 miles from Wentworth Falls, near Bedford Creek, 29 Nov. 1971, J. Pulley 877 (CBG 40518); Glen Elgin, 17 Feb. 1930, J.W. Haney 56 (CANB 6109); Beside Careys Peak Walking Track, Chichester State Forest, 24 March 1999, D.J. Mallinson 582 (CBG 99104351); Enmore State Forest, 29 Oct. 1990, S. McIntyre 1226 (NSW 243735).

2. Viola banksii K.R. Thiele & Prober, sp. nov.

V. hederacea Labill. affinis foliis grandioribus orbiculatis pluribus, sinu profundiore, floribus grandioribus colore diviore, petalo antico orbiculato plus minusve, glande antherae profunda et polline luteo vel aureo differt.

Typus: Australia, New South Wales, Cook's Rivulet, Kurnell, 12 Nov. 2001, K.R. Thiele 2671 & S.M. Prober (Holo: CANB; Iso: MEL, NSW, BRI)

V. hederacea var. elatines DC. Prodr. 1: 305 (1824); Erpetion reniforme Sweet, Brit. Fl. Gard. 2, t. 170 (1826); Viola reniformis (Sweet) Endl., Cat. Hort. Acad. Vindob. 1 (1842), non Wall. (1824); Viola hederacea f. reniformis (Sweet) Siebert & Voss, Vilmorin's Blumengartnerei 1 (1896). T: Botany Bay, R.Brown: ?BM (not found), n.v.

Vigorous perennial herb spreading by stolons; rootstock sometimes somewhat swollen and bulbous at the stem bases. Stems contracted so that the leaves form rosettes. Leaves broad-reniform to orbicular, the largest (12–)18–25(–35) mm long (from the base of the sinus to the apex of the lamina), (20-)30-45(-65) mm wide, 1.0-2.0 times wider than long, with a narrow basal sinus; lamina with (10-)12-18(-20) +/- prominent teeth, glabrous, +/- concolorous bright green; stipules narrowly triangular to broadly triangular, usually with several small or elongate, glandular teeth on each side. Flowers on scapes to 15 cm long and exceeding the leaves, strongly discolorous violet-and-white; anterior petal (7-)8-10(-12) mm long, (5-)6-8(-10) mm wide, distinctly and regularly ovate to broad-elliptic, broadest in the middle third, usually emarginate, with a large green Vshaped blotch at the base then rich violet for over half its length contrasting sharply with a prominent white apex, prominently 3-nerved, the midnerve not or scarcely anastomosing with the lateral nerves which branch +/- regularly towards the margins; lateral petals widely spreading, (8-)10-12(-14) mm long, strongly twisted to c. 180°, rich violet at the base grading to white distally; beard covering half or more of the width of the lateral petals; dorsal petals (8-)10-12(-15) mm long, (4-)6-8(-9) mm wide, ovate to broadly obovate, erect to strongly reflexed, rich violet at the flexure, white for most of

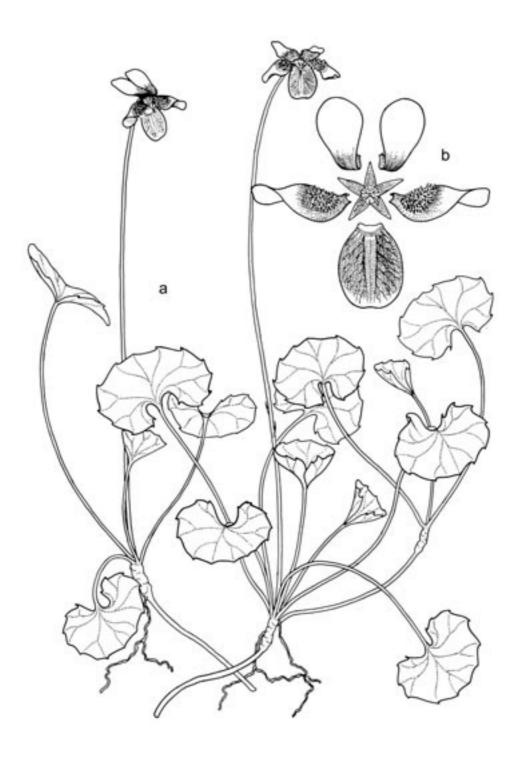


Figure 4. Viola banksii. a Habit x1; b Flower x2 (K.R. Thiele 2671, CANB).

their length. Anthers 2.0–5.0 mm long, cream, often flushed or flecked with violet, the terminal appendages straw-coloured, with short, irregular hairs on the outer margins of the anther cells; anther glands whitish green (never purplish), almost as long as the anther cells, very prominent, broad and high, +/- smooth; pollen and interior margins of the anther cells yellow to golden. Ovary and fruit whitish or pale green, often flecked or flushed purple; style distinctly geniculate at its insertion on the ovary. Seeds 1.8–2.5 mm long, glossy purplish-black, +/- smooth to irregularly rugose. Fig. 4.

Derivation of name. After Joseph Banks (1743–1820), naturalist on the Cook voyage to Australia and, with Daniel Solander, the first collector of the *Viola hederacea* species complex. The epithet *reniformis*, used for this species by some early authors, is preoccupied by *Viola reniformis* Wall., an Indian species.

Distribution and habitat. Common and widespread in near-coastal sites from near Ulladulla to just north of the Queensland-New South Wales border (Fig. 7b). Viola banksii is characteristic of coastal headlands, dune swales and coastal swamp and rainforest fringes, usually in moist areas. At some sites (e.g. at Pebbly Beach south of Ulladulla) V. banksii occurs on the margins of Acmena smithii rainforest behind the first dune, while V. hederacea occurs in drier sites beneath Eucalyptus maculata forest immediately adjacent. No intermediates between V. banksii and V. hederacea have been found, even in ecologically intermediate habitats.

Distinguishing features and variation. V. banksii differs from V. hederacea (Table 1; Fig. 3) in having larger, more richly coloured flowers, broad-ovate to broad-elliptic, almost semicircular anterior petals with triplinerved-pinnate rather than irregular venation, more strongly twisted, broader lateral petals with a more extensive beard, very large, prominent anther glands that are tall, broad and smooth, and purple-black seeds. Well-developed leaves of V. banksii are generally orbicular with a deep narrow sinus. Viola banksii matches most closely Viola hederacea 'forma G' of James (1990).

Adams (1982) described *Viola hederacea* subsp. *perreniformis* based on type material from Many Peaks Range, 40 km W of Gladstone, Queensland. This is a distinctive taxon found in inland, mostly mountain localities from the Border Ranges in southern Queensland to the Atherton Tableland. However, Adams included specimens referable to *V. banksii* in his concept of *V. hederacea* subsp. *perreniformis*, including the Banks specimen. *Viola hederacea* subsp. *perreniformis* differs from *V. banksii* in its smaller, less orbicular leaves with broader sinus, smaller flowers that are generally +/- concolorous pale violet, smaller, less prominent anther glands, and brown seeds.

Notes. Viola banksii was collected by Banks and Solander at Botany Bay in 1770, the first member of the *V. hederacea* species complex to be collected. Although a description and drawings were prepared for Banks' *Florilegium*, these were not published until 1900 (Banks & Solander 1900) when the taxon was ascribed to *V. hederacea*.

Banks and Solander collected mostly on the Kurnell Peninsula on the southern side of Botany Bay adjacent to the Endeavour anchorage. *Viola banksii* is still abundant on the banks of the small freshwater stream, Cook's Rivulet, from which the party drew water, and it is possible that this is the same population from which the Banks and Solander specimen was collected. The Cook's Rivulet plants are identical in all respects with the Banks and Solander specimen held at CANB.

Viola hederacea var. elatines DC., collected from Botany Bay by Robert Brown, appears to belong to this species. Microfiche photographs held at MEL of material from the De Candolle herbarium at G (not Type material, but presumably seen by De Candolle) show the characteristic orbicular leaves of the species. Viola banksii is common around Sydney and Brown would have had ample opportunity to collect material.

The excellent colour plate of *Erpetion reniforme* Sweet (basionym: *V. hederacea* var. *elatines*) in Sweet's British Flower Garden is not typical of the species, having leaves without deep sinuses and flowers with a rather rectangular to ovate anterior petal. It appears superficially closest to *V. eminens* (see below) or to an undescribed species found

on wet rock faces in the Blue Mountains and on Hawkesbury Sandstone as far south as Bundanoon. It is uncertain, however, whether material of these species could have been sent to Europe by 1826.

The plate of *Viola hederacea* in Banks and Solander (1900) comprises two illustrations of clearly different plants. The larger figure is *V. banksii*, clearly drawn from the Banks specimen collected at Botany Bay. The smaller figure is of *V. hederacea sens. str.*, presumably from material incorporated into the Banks herbarium after his return.

Viola banksii is commonly sold in the nursery trade (as *V. hederacea*), and is frequently grown in gardens well outside its natural range. In at least one locality (near Mt. Donna Buang, Victoria) it is adventive, presumably from material derived from a nearby garden or from dumped garden waste. It is likely that *V. banksii* will increase in range.

Selected specimens examined. New South Wales: Botany Bay, April 1770, J. Banks & D. Solander (CANB 371237); Durras, 24 Feb 1990, A.M. Lyne 116 (CBG 9013646); St. George's Basin, 24 Jan 1974, M. McMillan 740111 (CBG 56899); On the W side of Captain Cook Drive, 1.4 km from Cronulla High School, 19 Nov. 1986, M.M. Richardson 50 (CBG 8603640); Coffs Harbour, 13 May 1967, C.Burgess s.n. (CBG 17249); Arrawarra Headland N of Woolgoolga, 7 March 1997, A.R. Bean 11754 (BRI AQ654667); Iluka, 28 Dec. 1961, L. Pedley 941 (BRI AQ115419); 1.3 km S of Yamba towards Angourie, 12 Nov. 1994, A.R. Bean 8025 (BRI AQ633737); Norrie's Headland, Bogangar, 15 km S of Tweed Heads, 25 April 1976, G.N. Batianoff 12 (BRI AQ169594). Queensland: Between Mudjimbah and Mount Coolum, E of Nambour, 14 Aug. 1963, M.E. Phillips s.n. (CBG 23396); Eighteen Mile Swamp, North Stradbroke Island, 23 Nov. 1971, L. Durrington 650 (BRI AQ11278); Point Lookout, Stradbroke Island, 21 April 1935, D.A. Goy s.n. (BRI AQ115404); Nerang Creek, 1889, H. Schneider s.n. (BRI AQ115406); Southport, 28 Sept. 1952, A.B. Cribb s.n. (BRI AQ478596).

3. Viola eminens K.R. Thiele & Prober, sp. nov.

V. hederacea Labill. affinis foliis latioribus, habitu eminenti, scapis floribus longioribus, petalo antico ovato, colore florum diviore, glande antherae longiore et angustiore et polline luteo vel aureo differt.

Typus: Australia: Victoria: East Gippsland: Swamp on the Delegate River immediately upstream from its crossing with The Gap Road, c. 7.3 km direct line SW of Bendoc (37° 11' 58"S, 148° 49' 44"E), 5 Jan. 1997, *K.R. Thiele 2538 & S.M. Prober* (Holo: MEL; Iso: CANB, NSW, AD).

Perennial herb spreading by stolons; rootstock sometimes somewhat swollen and bulbous at the stem bases. Stems contracted so that the leaves form rosettes, or sometimes elongate (to 40 cm) with caulescent, alternate leaves. Leaves broad-reniform, the largest (10-)12-15(-25) mm long, (12-)25-35(-45) mm wide, 1.4-3.2 times wider than long, truncate at base or with a broad basal sinus; lamina with (6-)9-20 +/- prominent teeth, glabrous or with scattered unicellular hairs on the upper and/or lower surface, +/concolorous bright green; petioles 2–12 cm long; stipules narrowly triangular to broadly triangular, usually with several small or elongate, glandular teeth on each side. Flowers on scapes to 25 cm long and exceeding the leaves, usually strongly discolorous violetand-white, sometimes sub-discolorous (dark violet and pale violet); anterior petal (5-)8-10(-12) mm long, (3-)5-6(-9) mm wide, distinctly and regularly ovate to broadovate, broadest in the proximal third (or occasionally to near the middle), usually emarginate, with a large green V-shaped blotch at the base, then rich violet for over half its length contrasting sharply with a small white apex, prominently 3-nerved, the midnerve not or scarcely anastomosing with the lateral nerves which branch +/- regularly towards the margins; *lateral petals* widely spreading, (6–)9–11(–13) mm long, strongly twisted to c. 180°, rich violet at the base grading to white distally; beard covering half or more of the width of the lateral petals; dorsal petals (5-)10-12(-13) mm long, (2-)4-6(-7) mm wide, obovate to broadly obovate (rarely narrowly obovate), erect to

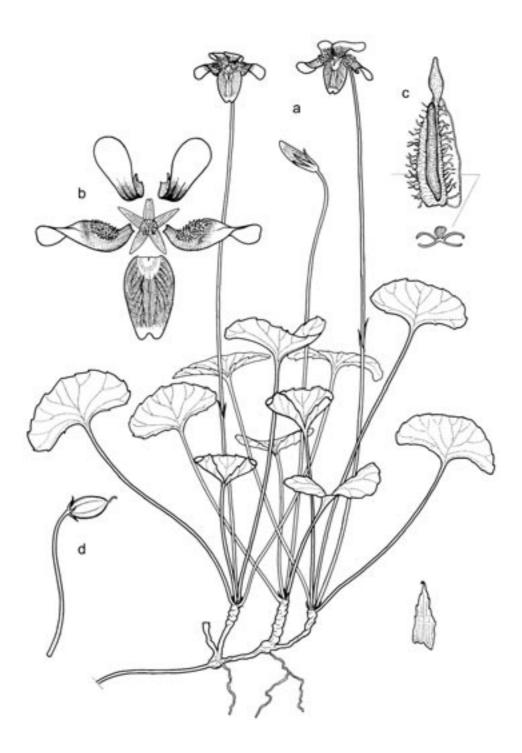


Figure 5. Viola eminens **a** Habit X1; **b** Flower X2; **c** ovary and style X?; **d** Fruit ?1 (K.R. Thiele 2538, CANB).

strongly reflexed, rich violet at the flexure, white for most of their length. *Anthers* 2.0–4.5 mm long, cream, often flushed or flecked with violet, the terminal appendages straw-coloured, with short, irregular hairs on the outer margins of the anther cells; *anther glands* whitish green (never purplish), almost as long as the anther cells, narrow and high, +/- smooth, not or scarcely flattened or depressed; *pollen* and interior margins of the anther cells yellow to golden. *Ovary* and *fruit* whitish or pale green, often flecked or flushed purple; *style* distinctly geniculate at its insertion on the ovary. *Seeds* 1.6–2.6 mm long, glossy purplish-black, +/- smooth to distinctly rugose. *Fig.* 5.

Derivation of name. From the Latin *eminens*, in reference to the distinctively tall, stately flowering scapes that are characteristic of the species.

Distribution and habitat. A common to abundant species in disjunct localities on the Fleurieu Peninsula in South Australia, in the Grampians and Otway Ranges in western Victoria, and from near Melbourne through eastern Victoria to far southern New South Wales (Fig. 7c).

In eastern Victoria *V. eminens* is a characteristic species of moist sites at high altitudes, from Toolangi and Mt Donna Buang to Mt Baw Baw and Mt Wellington, on Mt Buffalo, and in East Gippsland around the Errinundra Plateau. It has not been collected from the Cobberas Range, even though conditions there appear suitable. It almost always occurs in moist sites, either in moist grassland beneath snow gums or on the margins of swamps and in drainage lines. It is infrequent at lower altitudes (e.g. Den of Nargun, Mitchell River National Park near Bairnsdale).

At some sites (e.g. along moist road verges near Goonmirk Rocks, Errinundra Plateau, East Gippsland) *V. eminens* and *V. hederacea* grow in mixed swards, with the flowers of *V. eminens* borne characteristically higher (on longer scapes) than those of *V. hederacea*. No intermediates between them have been found, even in ecologically intermediate habitats.

In the Grampians Range *V. eminens* occurs in moist to very moist sites, e.g. along the banks of the McKenzie River at Zumsteins and on wet, dripping banks at Kalymna Falls. At both these sites *V. hederacea* grows in drier habitats close by the *V. eminens* populations. In South Australia it always occurs in moist sites along stream lines and in swamps, from the southern tip of the Fleurieu Peninsula (e.g. Tunkalilla Creek) north to the Barossa Valley and on Kangaroo Island.

Only two definite collections are known from New South Wales. At Glenbog State Forest, *V. eminens* occupies a small, swampy drainage line with e.g. *Gratiola peruviana*, *Ranunculus pimpinellifolius* and *Hydrocotyle spp.*, while *V. hederacea sens. str.* occurs immediately adjacent on the slopes of the stream gully in drier soil. At Nungatta Mountain it is found in a 'wet site in dry sclerophyll forest'. New South Wales specimens of *V. eminens* probably match 'forma C' of James (1990), although it does not occur on the North Coast as described for that form.

Distinguishing features and variation. Flowers of V. eminens are somewhat similar to those of the coastal V. banksii (Table 1; Fig. 3). They differ principally in the anterior petal being ovate (broadest toward the base) rather than almost orbicular (broadest about the middle), with a smaller white area at the tip, and in the smaller anther glands. Well-developed leaves of V. eminens are broader than long and have a broad sinus, while those of V. banksii are usually almost orbicular with a narrow sinus.

Distinguishing features from *V. hederacea sens. str.* are the taller flower-scapes, the richer violet flowers with a more definite demarcation between the violet and white, the distinctively neat, ovate anterior petal with triplinerved-pinnate rather than irregular venation, the more strongly twisted lateral petals with a more extensive beard, the narrower, less rugose, pale greenish-white anther-glands, the purplish-black seeds, and the broader, greener leaves. On herbarium specimens, leaves of *V. hederacea* often dry rather greyish and distinctly discolorous, while those of *V. eminens* remain pale green above and beneath.

Western collections of *V. eminens* (from the Grampians Ranges in Western Victoria and in South Australia) differ from eastern collections (east of Melbourne) in having a strong tendency towards caulescence. In the western populations, plants growing amongst dense vegetation along streamsides or in swamps often become scrambling or climbing, with elongate stems to 40 cm high and widely spaced, alternate leaves. In adjacent more exposed sites plants have contracted stems with leaves in fascicles. Caulescence has never been observed in *V. hederacea*, even in circumstances where plants are growing amongst dense vegetation, and has only rarely been seen in eastern *V. eminens*. It is possible that the western populations of *V. eminens* may warrant subspecific rank, but further work is needed to clarify their status.

A series of collections from near-coastal sites at the western end of Kangaroo Island have distinctively small, angular leaves. These plants are provisionally regarded as a coastal variant of *V. eminens*. Further work, however, may show them to be distinct.

Selected specimens examined. VICTORIA: 14 km S of Bendoc, Errinundra Flora Reserve, Goonmirk Rocks, 29 March 1988, G.A. Savage 17 (CBG 8800949); Valley below The Castle and near Whale Rock, Mt. Buffalo, 29 Dec 1952, R. Melville 2622 (MEL 525759); Near junction of Block 10 Road and Thompson Valley Road, 2 km from helipad, 9 Dec 1997, M.G. Corrick 11567 (MEL 2073182); Blue Range Road, near the crossing at Storm Creek, 2 Jan 1983, M.G. Corrick 8578 (MEL 657243); Blue Range Road, 1.5 miles N of Mt. Margaret Gap, Marysville district, 21 Dec 1965, E.J. Carroll s.n. (CBG 14407); On Ben Cairn Road, where it crosses Walker Creek, 200 m W from road to summit of Mt. Donna Buang, 20 Feb. 1996, D.B. Foreman 1737 (MEL 2044048); Mt. Baw Baw summit, 1 Feb. 1988, M. Gray 7153 (CANB 510168); Above Baw Baw Village, 31 Jan 1970, C.L. Gunn s.n. (CANB 251717); Echo Flat, Lake Mountain, 22 Dec 1965, E.J. Carroll s.n. (CBG 17933); Two miles from Toolangi toward Kinglake, E.J. Carroll s.n. (CBG 18007); Against falls at spillway to Lake St. George, Creswick, 30 Dec. 1971, J.H. Willis s.n. (MEL 100375); Otway State Forest, rest stop on road from Colac to Gellibrand, 6 km from Gellibrand, 12 Dec 1990, D. Cunningham 319 (MEL 288838); Top of Mount William and Mount Abrupt, Dec. 1856 - Jan. 1857, C. Wilhelmi (MEL 100422). South Australia: Section 748, Hundred of Moorooroo, Upper tributary of Tanunda Creek near Schlenke Gully, 25 July 1985, P.J. Lang 1702 (MEL 1598740; AD 98908074); Warren Conservation Park, 5 Jan 1986, R. Bates 6756 (CBG 9000713; AD 98607013); Barossa Valley, Upper Tanunda Creek, Schlenkes Creek Gorge, 24 Oct. 1984, D.N. Kraehenbuehl 4432 (CBG 8908345); AD 98449113); Mount Compass, 6 Oct. 1945, R.A. Perry (CANB 19535); Swamp North of Tunkalilla Beach, between Cape Jervis and Victor Harbour, 18 Nov. 1957, Hj. Eichler 14496 (CANB 389660; AD 95814014); Kangaroo Island, near the permanent pools of Rocky River at Shackle Road, 6 Jan. 1966, Hj. Eichler 18600 (CANB 318006; AD 96650349). New South Wales: N Slope of Nungatta Mountain, c. 48 km SSW of Eden, 16 Feb. 1984, T. James 511a (NSW); Glenbog State Forest, Packer's Swamp Road, at creek crossing 2 km SW of Robinson's Road junction, 29 Nov. 1998, K.R. Thiele 2609 (CANB).

4. Viola x zophodes K.R. Thiele & Prober, nothosp. nov.

Hybrida e V. eminente et V. fuscoviolacea, a primo floribus minoribus fuscatis, petalis in extremitatibus distalis non-albis vel dealbatis parum; a secundo floribus grandioribus in scapis longioribus fulcratis et foliis latioribus differt.

Typus: Australia: Victoria: East Gippsland: Swamp on the Delegate River immediately upstream from its crossing with The Gap Road, c. 7.3 km direct line SW of Bendoc (37° 11' 58"S, 148° 49' 44"E), 5 Jan. 1997, *K.R. Thiele 2539 & S.M. Prober* (Holo: MEL; Iso: CANB, NSW).

Perennial herb spreading by stolons; rootstock sometimes somewhat swollen and bulbous at the stem bases. *Stems* contracted so that the leaves form rosettes, never elongate with caulescent leaves. *Leaves* broad-reniform, the largest (10–)12–14(–16) mm long, (18–)20–28(–32) mm wide, 1.8–3 times wider than long, usually with a broad basal sinus; lamina with 12–18 +/- prominent teeth, glabrous or with scattered unicellular hairs on the upper surface, +/- concolorous bright green; petioles 2–4 cm long; *stipules*

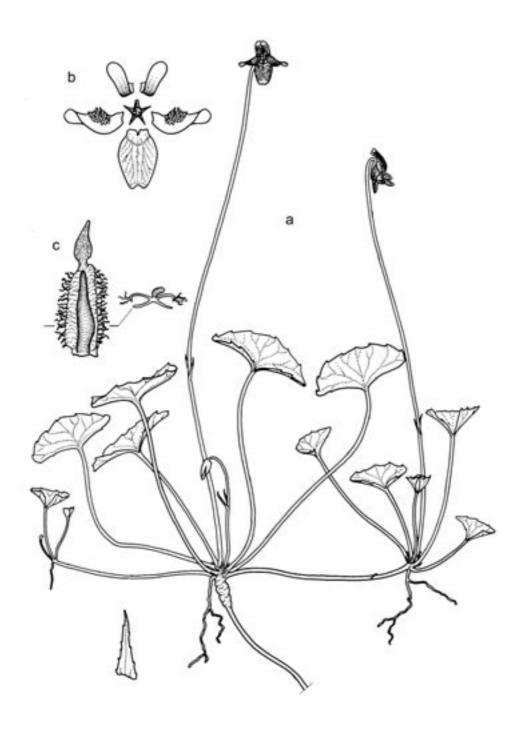


Figure 6. Viola x zophodes **a** Habit x1; **b** Flower x2; **c** ovary and style x? (K.R. Thiele 2539, CANB).

narrowly triangular, usually with several small, glandular teeth on each side. Flowers on scapes to 12 cm long and exceeding the leaves, blackish-violet with or without small whitish apices to the petals; anterior petal (6-)7-8(-8.5) mm long, (4-)5-6(-6.5) mm wide, distinctly and regularly ovate to broad-ovate, broadest in the proximal third, usually broadly emarginate, with a large green V-shaped blotch at the base, then blackish-violet for most of its length sometimes grading to a small whitish apex, prominently 3-nerved, the midnerve not or scarcely anastomosing with the lateral nerves which branch towards the margins; lateral petals widely spreading, (7-)7.5-8(-9) mm long, distinctly twisted to c. 180°, blackish-violet sometimes grading to white distally; beard covering about half the width of the lateral petals; dorsal petals (7-)8-9(-10) mm long, 3-4 mm wide, narrowly obovate, erect to strongly reflexed, blackish-violet with or without a whitish apex. Anthers 3.0–3.5 mm long, cream, often flushed or flecked with violet, the terminal appendages straw-coloured, with short, irregular hairs on the outer margins of the anther cells; anther glands green (never purplish), almost as long as the anther cells, +/- smooth, each somewhat flattened or depressed towards the other; pollen and interior margins of the anther cells white to cream. Ovary and fruit whitish or pale green, often flecked or flushed purple; style distinctly geniculate at its insertion on the ovary. Mature fruits and seeds apparently never produced. Fig. 6.

Derivation of name. From the Greek *zophodes*, 'dusky', 'gloomy' (as in twilight), in reference to the very dark, dusky-violet flowers.

Distribution. Scattered in moist sites in the highlands of Victoria e.g. Delegate River near Bendoc (East Gippsland), and near Mt Reynard and Mt. Wellington (Eastern Highlands). Viola x zophodes always occurs with V. eminens and V. fuscoviolacea, and may be expected in other montane to alpine sites where these species co-occur (Fig. 7d).

Distinguishing features and variation. Viola x zophodes is almost certainly an F1 hybrid between V. eminens and V. fuscoviolacea. It always occurs with these two species, usually occupying ecologically intermediate sites. At all known populations no seed is set, and the pollen grains are empty and ovules slightly discoloured at anthesis. For this reason, introgression with the parents apparently does not occur, and V. x zophodes forms a distinctive entity rather than a variable hybrid swarm. Plants are vigorously stoloniferous and often locally abundant.

V. x zophodes differs from V. eminens (Table 1; Fig. 3) in its smaller flowers that are blackish-violet compared with the bright violet of V. eminens, and in its narrower petals. It differs from V. fuscoviolacea in having larger, more openly presented flowers held above the leaves. V. fuscoviolacea leaves are usually smaller and more spathulate, but leaves on vigorous plants of V. fuscoviolacea are quite reniform and then indistinguishable from small leaves of V. x zophodes. The anterior petal of V. fuscoviolacea lacks the basal green crescentic mark seen on V. x zophodes (and all the other taxa described in this paper).

Different populations of *V. x zophodes* differ somewhat. For instance, on the Delegate River at The Gap Road (East Gippsland), plants are relatively tall and all petals have prominent, though small, white distal patches. Further downstream at the crossing of the Bonang-Bendoc road, and at the Lost Plain, the plants have slightly smaller flowers with very little white at all. Within a population there is little variation, suggesting that hybridisation events giving rise to *V. x zophodes* are rather rare, the plants propagating vegetatively. It is not known which is the male and which the female parent, or whether both crosses are possible.

Selected specimens examined. VICTORIA: Mount Reynard Plateau, c. 1 km NNW of Mt. Reynard, 14 Dec 2000, N.G. Walsh 5267 (MEL 2089855); Lost Plain, 7 miles NW of Mt. Wellington, 19 Jan 1967, T.B. Muir 4578 (MEL 100475); Delegate River, on flats at Bidwell Bridge, 1 Dec. 1962, J.H. Willis s.n. (MEL 100504).

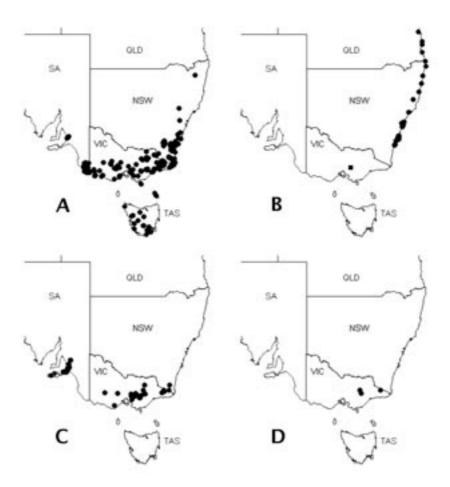


Figure 7. Distribution of *Viola* taxa in south-eastern Australia (based on specimen data from AD, BRI, CANB, MEL, NSW). **A** *V. hederacea sens. str.*; **B** *V. banksii* (● natural populations, ■ adventive population); **C** *V. eminens*; **D** *V. x zophodes*

Key to taxa in the V. hederacea species complex

The following provisional key includes all recognised taxa in the *Viola hederacea* species complex (except *V. hederacea* subsp. *curtisiae* and *V. improcera*), as well as a number of undescribed taxa that will be treated in subsequent papers.

V. hederacea subsp. *curtisiae* is described from high elevations at Mount Field in Tasmania; a few collections from the Baw Baw plateau in Victoria have also been allied to this taxon (Entwisle, 1996). *V. improcera* is known only from a few mountain peaks in Victoria (Nunniong Plateau and Mt. Useful) and the Australian Capital Territory (Brindabella Range). Both taxa are rarely collected, poorly understood, and of uncertain status. They could not be included in the key as their diagnostic features are uncertain.

- 1. Flowers on short scapes hidden among the leaves; petals scarcely exceeding the sepals2

2a.	Flowers white; lowland plants
3.	Well developed leaves twice as wide as long or wider; flowers concolorous pale bluish; stems often caulescent; habitat on sandstone in New South Wales
3a.	Leaves not much wider than long or, if about twice as wide as long then flowers distinctly discolorous
	Anterior petal +/- rectangular
5.	Flowers +/- concolorous pale blue; plants small, usually with cuneate leaf bases V . $sieberiana^2$
5a.	Flowers +/- discolorous pale and dark violet (or white and dark violet); plants robust, often trailing; leaves reniform
	Anterior petal broadest in the distal third, its venation usually somewhat irregular, petals with indistinct demarcation between violet and white colouration; seeds dull, cream to brown, usually mottled
6a.	Anterior petal broadest in the proximal third or the middle, regularly triplinerved, petals with distinct demarcation between violet and white colouration; seeds glossy purple-black
7.	Leaves usually +/- semi-circular, glabrous to sparsely hairy; flowers usually +/- discolorous; southern plants (S of the New England Tablelands, NSW)
7a.	Leaves suborbicular to reniform with a deep sinus, softly hairy; flowers +/-concolorous; northern plants (N from the NSW-Qld Border Ranges)
	Flowers blackish violet, with or without small white tips to the petals <i>x zophodes</i> Flowers bright violet and white, with prominent white (rarely pale violet) tips to the petals
9.	Anterior petal broadest in the middle; leaves reniform to orbicular, about as long as wide, often with a deep, narrow sinus; lowland, often coastal plantsV. banksii
9a.	Anterior petal usually broadest in the proximal third; leaves reniform, wider than long, with a broad sinus or truncate; alpine to montane plants in eastern Australia (at lower altitudes in SA)

¹A distinctive species from seasonally very dry sandstone sites in New South Wales including Jervis Bay, the Bundanoon area to the Blue Mountains with a disjunct population around Minyon Falls inland from Byron Bay.

²Including *V. hederacea* subsp. *seppeltiana*. *V. sieberiana* is restricted to sandstone sites around Sydney in New South Wales. *V. hederacea* subsp. *seppeltiana* is widespread from the Grampians Ranges (western Vic.) to the Mount Lofty Ranges (SA), and may be distinct from *V. sieberiana*. Specimens identified as *V. sieberiana* in intervening areas (e.g. eastern Victoria) are misdetermined, most being *V. fuscoviolacea*, *V. cleistogamoides* or small-flowered *V. hederacea*.

³A provisional taxon found on moist sandstone sites particularly on waterfalls and wet soakage areas on sandstone in NSW from Bundanoon to the Blue Mountains.

⁴Preliminary results suggest that this taxon should be raised to species rank, as it is geographically and morphologically distinct from *V. hederacea sens. str*.

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