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Grammosolen (Solanaceae - Anthocercideae) revisited

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Abstract: Study of newly collected specimens from beyond the former known geographical range of *Grammosolen*, together with consideration of newly published results of molecular phylogenetic studies in tribe Anthocercideae have led to an expanded concept of the genus. The rare *G. archeri* Haegi is newly described from far south-eastern Western Australia; *G. odgersii* is transferred from *Cyphanthera*; and the known range of *G. truncatus*, formerly regarded as an endemic South Australian species, is extended to adjacent far eastern Western Australia.

Keywords: *Grammosolen*, *Cyphanthera*, Anthocercideae, Solanaceae, taxonomy, new species, intergeneric hybrids

Introduction

Grammosolen Haegi was first described as a new genus in the context of a monographic study leading to the re-instatement of the distinctively Australasian tribe Anthocercideae G.Don (Haegi 1981, 1983). The study led to the recognition of 31 species in seven genera–*Anthocercis* Labill., *Anthotroche* Endl., *Crenidium* Haegi, *Cyphanthera* Miers, *Duboisia* R.Br., *Grammosolen* and *Symonanthus* Haegi (Haegi 1981, 1983). *Grammosolen* was established to accommodate two closely related, distinctive species: *G. dixonii* (F.Muell. & R.Tate) Haegi (formerly mistakenly assigned to *Newcastelia* F.Muell. in family Verbenaceae) and *G. truncatus* (Ising) Haegi, originally described as a species of *Anthotroche*. One new species has since been described in each of *Anthocercis* (Macfarlane & Wardell-Johnson 1996) and *Duboisia* (Craven *et al.* 1995), bringing the total to 33 species in the tribe.

Grammosolen has been known only from the state of South Australia. Additional collecting in more remote parts of Australia has since not only extended the known distribution in South Australia but has also brought to light specimens from Western Australia. Some of these represent a range extension of *G. truncatus* a relatively short distance across the border from South Australian populations nearby. Others, confined to a small area much further west, inland from Cape Arid on the southern coast, have proved to be not readily assignable to either existing species, or to any other species in the tribe. These specimens are consistently distinct in several features, including their small, orbicular-reniform to obcordate leaves and in their smaller flowers and fruits. The new species *Grammosolen archeri*, endemic to south-eastern Western Australia, is described here on the basis of these specimens.

Materials and Methods

This study is based on investigations carried out over several decades, commencing in the first instance as part of the subject of a PhD thesis (Haegi 1983). It is based on detailed morphological examination of all available herbarium material in Australian and relevant overseas herbaria as well as many specimens collected in the course of the study. Measurements of each character used in the descriptions were, where possible, taken from a sample of between 20 and 30 specimens selected to represent the whole geographic range. Characters which showed variability were measured for at least two organs on each specimen in the sample and in the case of leaves, the dimensions of the largest as well as of two or three of those judged to be close to the mode were recorded. Dried material was used for all measurements, except the flowers which were either softened in a weak solution of detergent and hot water or for which spirit material collected in the course of the study was used. Leaves were measured to the nearest millimetre with a ruler, while most other organs were measured to the nearest ½ millimetre using a low-power stereo-microscope fitted with an ocular micrometer, at 10× magnification. Larger hairs (1.0–2.5 mm long) were measured in this way to the nearest 0.05 mm; smaller hairs (0.025–0.075 mm) were measured to the nearest 0.025 mm at 40× magnification. Indumentum terminology follows Haegi (1991).

Chromosome numbers were investigated for three species from the study of meiosis in pollen mother cells. To date it has not been possible to obtain living material of the fourth species, *G. archeri*. Flower buds collected in the field were placed immediately in a mixture of 3 parts of ethanol to 1 part of glacial acetic acid (mixed in situ). After 24 hours the buds were transferred to 100% ethanol, kept in cool conditions and finally

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stored in temperatures below 0°C. Standard anther squash techniques (Darlington & La Cour 1970) were used to obtain microscope slide preparations for observing chromosomes at meiosis. The preparation was examined with a compound light microscope at up to 1,000× magnification, sometimes with the aid of phase contrast illumination. The results were recorded using a camera lucida device fitted to the microscope.

Although it can be caused by other factors (such as environmental ones) sterility of pollen is a useful guide to the occurrence of hybridisation, especially when pollen from possible parents sampled at the same time proves highly viable. Stainability of pollen was tested as an indicator of viability using 0.5% lactophenol cotton blue, which stains cytoplasm. Pollen from a single mature anther from each of several different flowers from recently collected herbarium specimens was teased out into a drop of stain on a microscope slide, a coverslip was applied and the preparation examined with a compound microscope, with all grains present scored.

The composite distribution map (Fig. 3) was prepared utilising point distributional data from the AVH, viewed in the ALA portal (accessed 3 July 2019), downloaded and edited to remove misidentified and misplotted duplicate records. The map as presented was prepared using QGIS v. 3.2.0–Bonn, with the map outline and features (coastline, sand-ridge and lakes layers) from GEODATA TOPO 250K series 3 Topographic data (Geoscience Australia 2018, accessed 5 February 2018).

Generic placement of *Cyphanthera odgersii*

When it was described, *Grammosolen* was unique within the Anthocercideae for the occurrence of multangulate hairs (in particular on the exterior of the corolla lobes), a di- or tri-dynamous androecium of five fertile stamens and a gametic chromosome number of n=56. At that time attention was drawn to some close similarities between *Cyphanthera odgersii* (F.Muell.) Haegi and the two known species of *Grammosolen*. Verticillately-branched trichomes are found in both *C. odgersii* and *G. dixonii*, while all three species share a spike-like inflorescence and, perhaps most notably, hippocrepiform anthers (Haegi 1983). These last two features are not otherwise found in *Cyphanthera* (Haegi 1983). However, like all species of *Cyphanthera* for which a count had been determined (*C. albicans* (A.Cunn.) Miers, *C. microphylla* Miers, *C. myosotidea* (F.Muell.) Haegi and *C. tasmanica* Miers), *C. odgersii* has a gametic chromosome number of n=30 (Haegi 1983). On balance, *C. odgersii* was included within *Cyphanthera* rather than in *Grammosolen* for that reason and because it shared with all the other species a corolla glabrous outside and a didynamous androecium of only four stamens. This classification has been widely adopted since that time.

More recently, molecular phylogenetic studies of the Anthocercideae and near relatives, analysing sequence data from four chloroplast DNA regions — *ndh*F and *trn*L/F (Garcia & Olmstead 2003), as well as *trn*S-G and *mat*K (Clarkson *et al.* 2004) — have provided new evidence for assessing the affinities and relationships of these genera. It is now generally accepted that together with the genus *Nicotiana*, these genera make up a distinctive grouping within the family, for the time being treated as subfamily Nicotianoideae. This is confirmed and placed within the context of an overview of the molecular phylogeny of the Solanaceae as a whole by Olmstead *et al.* (2008). There is strong support for continued recognition of Tribe Anthocercideae (Clarkson *et al.* 2004), perhaps with some uncertainty about the placement of the genus *Symonanthus*, whose relationships with the remainder of the Anthocercideae on the one hand and *Nicotiana* on the other, remain unresolved (Olmstead *et al.* 2008). Within the Anthocercideae these molecular phylogenetic studies provide partial support for the morphologically-based generic classification (including continued generic recognition of *Grammosolen*) but also provide evidence for a different approach to the circumscription of some genera. On the basis of that evidence *C. odgersii* is demonstrated, as part of a highly supported "*Grammosolen* clade", to have a closer relationship with the two known species of *Grammosolen* than to all the other species of *Cyphanthera* (Garcia & Olmstead 2003; Clarkson *et al.* 2004).

The evidence from molecular studies prompts a re-assessment of the diagnostic value of characters found in *Grammosolen* and *Duboisia*/*Cyphanthera*. Inclusion of *Cyphanthera odgersii* in the *Grammosolen* clade on molecular grounds is consistent with the shared occurrence of erect, hippocrepiform anthers dehiscing by a hippocrepiform slit on the abaxial face (Figs 1, 10, 11). This may prove to be a synapomorphy for the expanded genus (together with the otherwise distinctive genus *Anthotroche*). In the apparent plesiomorphic condition found throughout *Duboisia* (four species) and the remainder of *Cyphanthera* (eight species) the anthers are sub-reniform, oblique (twisted towards the vertical and tilted abaxially) and dehisce by a semicircular slit along the distal margin (for example as in *C. racemosa* (F.Muell.) Haegi – Fig. 1). While a dense indumentum of dendritic hairs occurs in some species of *Cyphanthera*, the very dense woolly indumentum found in *C. odgersii* is unique in the genus (Haegi 1991). Similar hair-coverings are, however, found in *Grammosolen* and *C. odgersii* shares elaborate verticillately branched hairs with *G. dixonii*. Similarly the spike-like inflorescence of *C. odgersii* is unique in *Cyphanthera* but occurs in all species of *Grammosolen*, being particularly well developed in *G. dixonii*. Flowers with only four fertile didynamous stamens are characteristic of all *Cyphanthera* species. In *Grammosolen* the androecium consists of five fertile, di- or tri-dynamous stamens; this is probably the plesiomorphic condition. If *C. odgersii* is correctly placed in *Grammosolen*, it is possible that the loss of the fifth fertile stamen arose independently

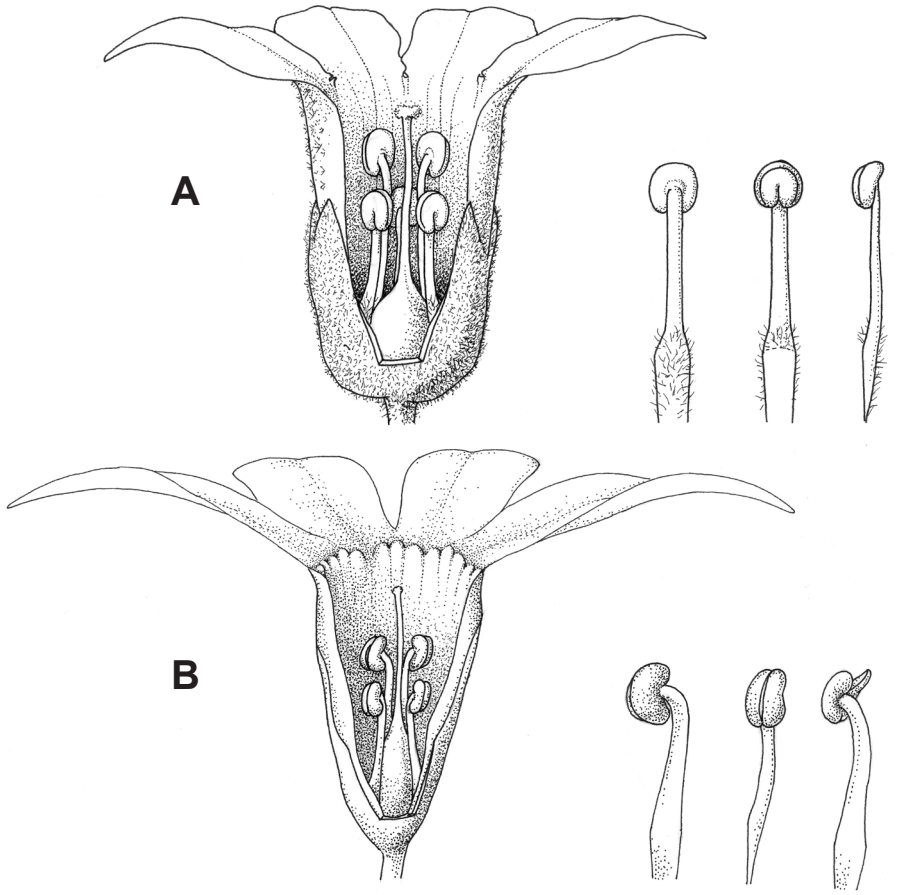

Fig. 1. Semi-schematic representation of anther types in *Grammosolen* and *Cyphanthera*, showing flowers with part of calyx and corolla removed to reveal stamens, together with excised stamens depicting dorsal (abaxial), ventral (adaxial) and lateral views of anthers. **A** *Grammosolen* (*G. dixonii – Haegi 868G*, × 8.5); **B** *Cyphanthera* (*C. racemosa* (F. Muell.) Haegi – *Haegi 1957* (NSW, CBG, PERTH), × 7). Illustration by R. Roden.

in this species, separately from the event which resulted in this condition in *Cyphanthera* and *Duboisia*. Alternatively, the presence of a fifth fertile stamen in the other three species of *Grammosolen* could represent a reversion. The ontogenetic likelihood of such a reversion would require further investigation. Some insight may be evident in the variable occurrence of flowers with four or five fertile stamens in the related species *Crenidium spinescens* Haegi: the absence of one of the fertile stamens could be the result of genetic masking rather than its irreversible loss.

The multangulate hairs found in all species of *Grammosolen*, but absent throughout *Cyphanthera*, may have been secondarily lost in *C. odgersii* as a member of the *Grammosolen* clade or may have evolved subsequently in the other species. Chromosome numbers in the tribe were first counted by Barnard (1949) who recorded n=30 and 2n=60 for *Duboisia leichhardtii* and *D. myoporoides*. Ikanaga *et al.* (1979) added a count of n=?28 for *D. leichhardtii* and confirmed n=30 for *D. myoporoides*. Further investigations by Haegi (1981, 1983), resulted in the first chromosome number determinations for *Symonanthus*, *Anthocercis*, *Cyphanthera*, *Grammosolen*, *Anthotroche* and *Crenidium*. To the extent that counts were obtained (for 21 of the 31 species), a strong correlation was demonstrated with morphological features characterising genera (Haegi 1981, 1983). A gametic chromosome number of n=30 was observed for five of the nine species of *Cyphanthera* (including *C. odgersii*) while the only two species of *Grammosolen* known at the time produced counts of n=56 (Haegi 1983). Given it seems likely that n=56 represents the derived state, the occurrence of the plesiomorphic state in the clade (n=30 in *C. odgersii*) is not problematic.

On the basis of the compelling evidence from the molecular phylogenetic studies and the assessment above, *C. odgersii* is here transferred to *Grammosolen*, with the generic circumscription emended accordingly. This transfer creates no nomenclatural problems at any level. The species epithet has not been used previously in *Cyphanthera* and the lectotype species of the genus designated by Hunziker (2001) is *C. ovaliflolia* Miers (currently regarded as a taxonomic synonym of *C. albicans* (Cunn.) Miers subsp. *albicans*; Purdie *et al.* 1982; Haegi 1983).

Occurrence of putative intergeneric hybrids in the Anthocercideae

The possible occurrence of several intergeneric hybrids was recorded by Haegi (1983) and investigations of the alkaloid chemistry of some of these putative hybrids, together with the putative parents (El Imam *et al.* 1991) provided supporting evidence. Two of the recorded hybrids involve *Grammosolen*, with one species, *G. dixonii*, being one of the putative parents in each instance. This is reported on in more detail under *G. dixonii* below.

Taxonomy

Grammosolen Haegi

Telopea 2 (1981) 178. — **Type species:** *Grammosolen dixonii* (F. Muell. & R.Tate) Haegi

Newcastelia auct. non F.Muell.: F.Muell. & Tate, *Trans. & Proc. Roy. Soc. S. Austral.* 10 (1888) 81, p.p. as to *N. dixonii* (= *Grammosolen dixonii*); J.M.Black, *Fl. S. Austral.* 3 (1926) 479, p.p. as to *N. dixonii*, excl. W.A. material; C.A.Gardner, *Enum. Pl. Austral. Occ.* 3 (1931) 111, p.p. as to *N. dixonii*, excl. W.A. material; J.M.Black, *Fl. S. Austral.* edn. 2, 4 (1957) 721, p.p. as to *N. dixonii*, excl. W.A. material; Beard, *Descr. Cat. W. Austral. Pl.* (1965) 92, p.p. as to *N. dixonii*, wrongly recorded for W.A.

Anthotroche auct. non Endl.: Ising, *Trans. & Proc. Roy. Soc. S. Austral.* 46 (1922) 605, t. 38, 39, Fig. 1, p.p. as to *A. truncata* (= *Grammosolen truncatus*); J.M.Black, *Fl. S. Austral.* 3 (1926) 500, p.p. as to *A. truncata*; *Fl. S. Austral.* edn 2, 4 (1957) 754, p.p. as to *A. truncata*; N.T.Burb., *Dict. Austral. Pl. Gen.* (1963) 20, p.p.; H.Eichler, *Suppl. J.M. Black's Fl. S. Austral.* (1965) 226, 273, p.p. as to *Newcastelia dixonii* and *Anthotroche blackii* as applied to S.A. specimens including all those cited; D'Arcy in Hawkes, R.N.Lester & A.D.Skelding, *Biol. Taxon. Solanac.* (1979) 12, 14, 17, 21, p.p.; Haegi, ibid, 121–124, p.p.

Anthocercis auct. non Endl.: F.Muell., *Fragm.* 10 (1876) 19, p.p. as to *A. odgersii* (= *Grammosolen odgersii*, q.v.).

Cyphanthera auct. non Miers: Haegi, *Telopea* 2(2) (1981) 177; R.W.Purdie, Symon & Haegi, *Fl. Austral.* (1982) 27; Hunziker, *Gen. Solanac.* (2001) 386–388, all p.p. as to *C. odgersii* (= *Grammosolen odgersii*).

Erect ± leafy, taprooted *shrubs*, suckering from stem base following damage to or removal of aerial parts, densely tomentose with variously dendritic hairs on all vegetative parts, with corky fissured bark at stem base. *Leaves* alternate, petiolate to subsessile, entire. *Flowers* bisexual, protogynous, subtended by a pair of opposite or sub-opposite bracts, borne in leafy clusters of cymes terminating condensed lateral branchlets, shortly pedicellate. *Calyx* ± cyathiform, 5-lobed, persistent, lanate-tomentose. *Corolla* ± narrowly tubular with ± regular (4–) 5 (–6)-lobed patent limb, drab white with violet striations in throat [but unknown in *G. archeri*], glabrous or glandular-hairy outside, glabrous inside except for the very densely and minutely papillose lobes; *aestivation* of lobes ± induplicate, the margins of each lobe overlapping each other or ± meeting, the lobes free and erect; *tube* ± narrowly funnel-shaped; *lobes* broadly ovate to narrowly elliptic with truncate base, very densely and minutely papillose on upper (inner) surface, otherwise glabrous. *Stamens* epipetalous at base of corolla-tube, 4 or 5, usually didynamous, very rarely tridynamous, slightly recurved prior to and ± erect at anthesis, included in the corolla-tube; *anthers* much shorter than filaments, unilocular, free, erect, hippocrepiform, dehiscing by an abaxial hippocrepiform slit. *Ovary* 2-locular, surrounded at base by a moist, annular, aromatic but non-nectariferous disc; *ovules* few; *style* included; *stigma* ± capitate, very shortly bilobed. *Fruit* a smooth capsule with marginicidal and loculicidal, septifragal dehiscence into 4 valves, somewhat concealed by the dense, long indumentum of subtending branchlet and calyx; *calyx* non-accrescent but as long as or longer than capsule; *seeds* few, subreniform with reticulate testa; *embryo* slightly curved, not coiled. *Gametic chromosome number* (determined for three of the four species) 30 or 56.

Distribution. As newly circumscribed, *Grammosolen* is a genus of four species; these have non-overlapping ranges, extending from the Avon Wheatbelt through the Coolgardie, Great Victoria Desert and Mallee regions in southern Western Australia, to the Great Victoria Desert, western Gawler Ranges, Eyre Yorke Block and the Murraylands in South Australia. All of the species occur as scattered, small populations on local patches of sandy

Key to species

1. Leaves 2.5–7 mm long, orbicular-reniform to obcordate (sometimes broadly ovate at shoot tips), L:B mostly 0.65–0.96; calyx 2.0–2.5 mm long . . . . . **3. *G. archeri***

1: Leaves 7–30 mm long, ovate, ovate-elliptic, ovate-triangular (sometimes broadly so) or subcordate, L:B mostly 0.8–3.8; calyx 2.5–7 mm long

2. Leaves conspicuously petiolate, with petiole 2–4 mm long; leaf base cuneate; indumentum very densely and closely tomentose with multangulate-dendritic hairs 0.05–0.15 mm long above and below . . . . . **2. *G. truncatus***

2: Leaves of subsessile appearance, with petiole 0.5–1.5 mm long, rarely 3 mm long in larger leaves; leaf base rounded-truncate, cordate, cuneate or attenuate; indumentum densely to very densely tomentose to lanate-tomentose with multangulate-dendritic and verticillately-branched hairs 0.2–1.0 mm long

3. Leaves ovate-triangular to very broadly so, sometimes subcordate; base rounded truncate, sometimes cordate or broadly cuneate; multangulate-dendritic and verticillately-branched hairs both present; leaves appressed or distally inclined, more or less overlapping; corolla lobes mostly 3–6 mm long; stamens 5 . . . . . **1. *G. dixonii***

3: Leaves broadly to narrowly elliptic, base cuneate to attenuate; indumentum consisting entirely of verticillately branched hairs (other than small, inconspicuous glandular hairs); leaves spreading; corolla lobes 1.3–2.5 mm long; stamens 4 . . . . . **4. *G. odgersii***

soil or in extensive dune systems, generally on disturbed sites within or in association with mallee vegetation.

1. *Grammosolen dixonii* (F.Muell. & R.Tate) Haegi

Telopea 2 (1981) 178; R.W.Purdie, Symon & Haegi, *Fl. Austral.* 29 (1982) 29; Haegi in Jessop & Toelken, *Fl. S. Austral.* edn 4, 3 (1986) 1242. — *Newcastelia dixonii* F.Muell. & Tate, *Trans. & Proc. Roy. Soc. S. Austral.* 10 (1888) 81, as '*Newcastlia Dixoni*'. — **Type citation:** "On sand ridges at Ral-Ral on the River Murray, 30 miles [c. 48 km] from the Victorian border; also at Crystal Brook; Mr Samuel Dixon." **Lectotype (here designated):** Ral Ral, S.A., *S. Dixon s.n.* (MEL41019). **Isolectotypes:** AD97221081A, BM629250. **Remaining syntype:** Crystal Brook, S.A., *S. Dixon s.n.* (AD97221081B).

Anthotroche blackii auct. non F.Muell.: H.Eichler, *Suppl. J.M. Black's Fl. S. Austral.* (1965) 273, p.p. as to all S.A. specimens cited.

Erect, spreading or sprawling greyish *shrub* 0.3–2 m tall and 0.8–3 (–5) m diam., with branches (at least finally) ascending. *Branches* very densely lanate-tomentose with multangulate-dendritic and verticillately branched hairs mostly 0.6–1.3 mm and fewer hairs c. 1.5 times as long as these i.e. 0.8–1.5 mm, and scattered, inconspicuous glandular hairs 0.1–0.4 mm, the indumentum gradually wearing off with age. *Leaves* loosely appressed or at least distally inclined, more or less overlapping so as to obscure much of the axis, subsessile or with a petiole to 1.5 (–3) × 1 mm; *lamina* ovate-triangular to very broadly so, sometimes subcordate (L:B (0.8–) 0.9–1.5 (–2.5)), (6–) 8–16 (–20) × (4–) 6–15 (–17) mm, densely to very densely tomentose (including petiole) with stalked multangulate-dendritic and verticillately branched hairs, mainly 0.1–0.3 mm and fewer 0.2–0.5 mm, and scattered inconspicuous glandular hairs, 0.05–0.1 mm, the branched hairs usually denser and up to 0.5 (–0.7) mm on the underside; *base* rounded-truncate, sometimes cordate or broadly cuneate; *apex* acute or slightly obtuse, less commonly acuminate, usually angular or blunt, rarely rounded; *margin* flat or often undulate, sometimes slightly recurved; midrib obscure adaxially, slightly prominent abaxially. *Flowers* borne in leafy clusters consisting of one to three, 1–3-flowered cymes on much-condensed lateral branchlets, sometimes aggregated to form leafy spikes; *inflorescence-bracts* 1–4 × 0.5–2 mm, moderately tomentose with multangulate-dendritic hairs. *Pedicel* 0.2–0.8 mm, oblique, glabrous. *Calyx* 3.3–5 mm, outside densely to very densely tomentose with eglandular multangulate-dendritic and verticillately branched hairs 0.2–0.3 (–0.8) mm and upper layer 0.4–0.8 (–2.0) mm, inside moderately pubescent with porrect to antrorse glandular hairs 0.05–0.15 mm, and multangulate-dendritic, forked or simple eglandular hairs 0.15–0.3 mm on the lobes, often only near the apex; *calyx-lobes* acute to slightly obtuse or rarely acuminate, always angular, (0.4–) 0.5–1.1 (–1.5) times as long as tube, 1.0–2.5 (–3) × 1–1.5 mm, sinuses acute. *Corolla* (7.5–) 8–12.5 mm, dull white with violet striations, outside moderately pubescent with multangulate-dendritic hairs 0.2–0.3 (–0.4) mm on the lobes and upper tube, inside very densely papillose with hairs 0.05–0.1 mm on lobes; *tube* 4.5–7.5 mm long., diam. 1.0–1.7 mm at base, 2.5–3.5 mm at limb-base; *lobes* ovate to elliptic with truncate base, (L:B 1.4–2.2 (–2.8)), 3–6 (–7.5) × (1.6–) 2–4 mm, slightly narrowed or broadened at the base, apex acute and usually blunt or rounded, rarely angular, margin flat. *Stamens* 5, the longer ones (3.5–) 4–5 mm and the shorter ones 2.5–3.5 (–4.2) mm; *filament-bases* and adjacent corolla moderately to densely pubescent with simple or forked eglandular hairs 0.2–0.5 (–0.8) mm, less dense abaxially; *anthers* 0.8–1.0 × 0.8–1.0 mm. *Ovary* very broadly ovoid to globose or depressed globose,

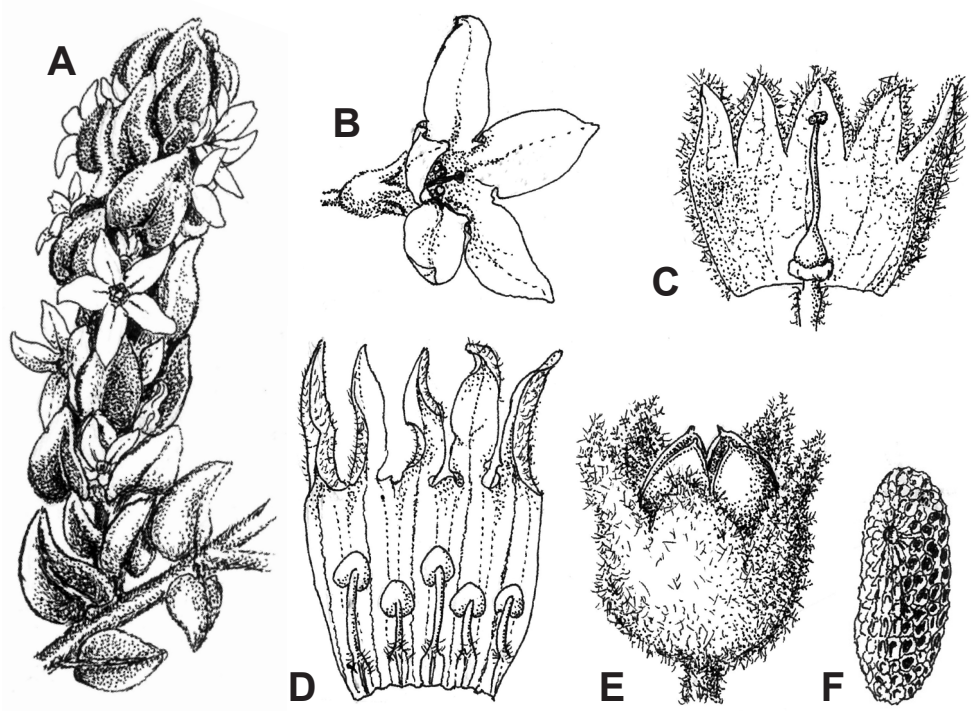

Fig. 2. *Grammosolen dixonii*. **A** flowering branchlet, × 1; **B** flower, × 2.5; **C** calyx of advanced bud opened out, with pistil, × 6; **D** opened corolla of same, × 6; **E** capsule, × 6; **F** seed, × 10. (A–D *Haegi 1331*; E–F *Haegi 869*). Illustration by M. Perkins.

0.6–1.2 × 0.6–1.2 mm; *ovules* 4–9 in total; *style* 2.7–3.5 (–4.2) mm, ± equal to the longer stamens and included by 0.5–2 mm; *stigma* c. 0.2 × 0.4 mm; *disc* undulate, 0.2–0.5 mm high, usually slightly, rarely much greater in diameter than the ovary (to 1.6 mm), red. *Capsule* ± inconspicuous, ± embedded in dense long hairs of enclosing calyx and axis, ± globose, 3.5–4.5 × 3–4.8 mm. *Seeds* 1–5, 2.5–3.5 × 1.1–1.6 mm; *surface-reticulae* 0.1–0.35 × 0.1–0.2 mm. *Chromosome number:* n=56 (*L. Haegi 676, 1457M*). **Fig. 2.**

Typification. This species was described (under the basionym, *Newcastelia dixonii*) by two authors, F. Mueller and R. Tate, and two localities are given in the protologue. Material corresponding with information in the protologue has been located on three sheets, one each in AD, BM and MEL. But for one piece on the AD sheet, these specimens all match one another and resemble material from the stated area of collection, viz. Ral-Ral on the River Murray. Although not labelled as such, the distinctive piece on the AD sheet, as indicated by the more distinctly cordate leaves and undulate leaf margins, resembles material known from the present study to be restricted to the northern Yorke Peninsula region and Crystal Brook area. This specimen is almost certainly that referred to in the protologue as having been collected at Crystal Brook. One syntype collection, therefore, is in fact divided so that part is mounted on each of three sheets (AD, BM, MEL) while the other collection consists of a single piece on the AD sheet. The specimen MEL41019 is designated Lectotype; it bears a label in Mueller's hand and is the most ample specimen. It had been labelled (mistakenly in light of the foregoing discussion) as a holotype.

Distribution and Ecology. Known only from South Australia where it occurs in scattered populations at similar latitudes, in three main areas: on northern Eyre Peninsula; northern Yorke Peninsula together with the adjacent northern plains west of the southern Flinders Ranges and northern Mount Lofty Ranges; and east of these ranges, in an area on both sides and in the vicinity of the River Murray (Fig. 3).

Grammosolen dixonii is found almost exclusively on calcareous pale red sandy soils in mallee vegetation and is frequently associated with *Triodia*. It is generally a plant of disturbed sites, which promote seed germination and may be locally frequent following fire. Mechanical damage or burning of the aerial parts may stimulate the production of suckers from the stem base.

Phenology. Flowering specimens have been collected in all months except February, May and June, with most from August to January. Fruiting specimens have been collected from November to January. Galling of fruits as a result of insect attack is a common occurrence.

Conservation status. *Grammosolen dixonii* is relatively rare, with many populations occurring in depleted remnant vegetation on roadsides in agricultural areas. Populations are conserved in several reserves such as the Lake Gilles, Clements Gap, Pooginook and Cooltong Conservation Parks.

Diagnostic features. *Grammosolen dixonii* is clearly distinct from the other species in the genus, on account of its ovate-triangular to sub-cordate leaves and the combination of stalked multangulate-dendritic and verticillately branched hairs on the axes and leaves. There is no intergradation with other species, though in the vicinity of Kyancutta on Eyre Peninsula, populations at the north-western extreme of the range of *G. dixonii* closely approach, within 25 km, populations at the furthest south-eastern extent of the occurrence of *G. truncatus*.

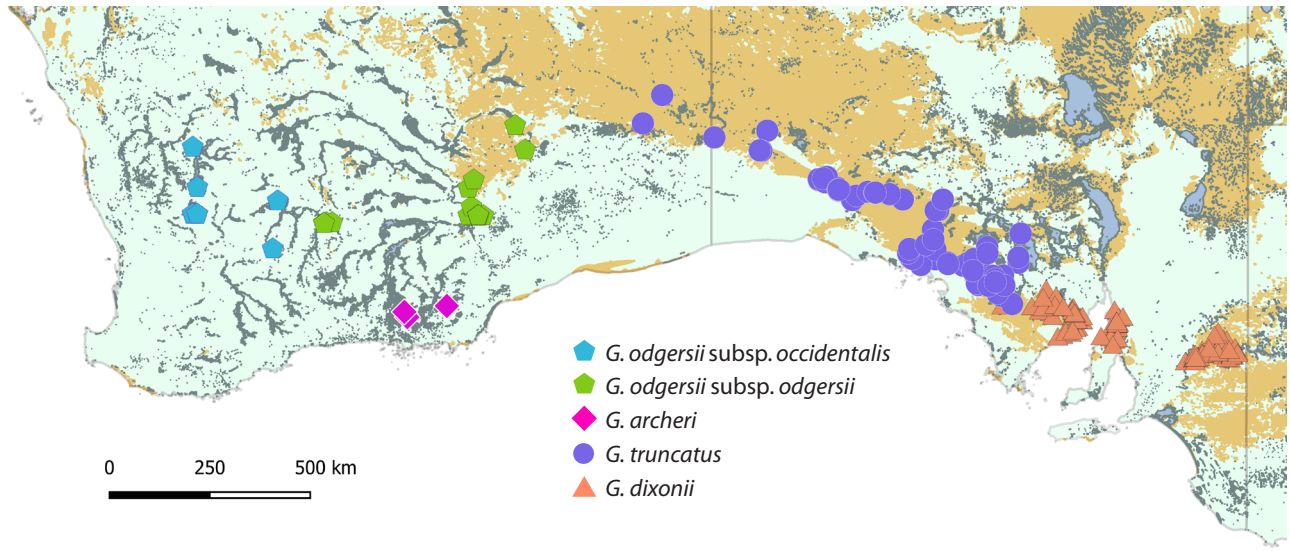

Fig. 3. Southern (central and western) Australia, showing the geographical occurrence of 4 species of *Grammosolen*, including two subspecies (from AVH, ALA–accessed 3 July 2019 and corrected) in relation to extent of sand-ridges (tan) and lakes/drainage systems (grey).

Variation. Plants with acuminate (rather than acute) leaf apices, undulate margins and less dense indumentum predominate in the northern Yorke Peninsula populations; similar specimens are rare elsewhere. Leaves are mostly in the range 8–16 × 6–15 mm, but plants with smaller leaves are found mainly on Eyre Peninsula (e.g. *Orchard 2935*, leaves 7 × 6 mm) while the largest-leaved plants occur on Yorke Peninsula (e.g. *Copley 144*, leaves to 20 × 17 mm). Slight zygomorphy of the corolla is apparent in some plants seen in the fresh state (e.g. *Haegi 1331*, from Northern Lofty Region). Two of the lobes assume an upper, more vertical position and may be slightly closer together, while the remaining three lobes are oriented more horizontally, though not otherwise differently positioned than in regular flowers. There is insufficient correlation of variation in any of these characters either with other characters or geographically for the recognition of any infraspecific taxa.

Derivation of name. Named for Samuel Dixon, an Adelaide geologist and naturalist who had a special interest in fodder plants and collected the type material in the 1880's (see Sharr 1978).

Selected specimens (145 examined)

SOUTH AUSTRALIA. **Eyre Peninsula:** 29.5 km E of Kimba, 4.x.1975, *R.J. Chinnock 2747* (AD); Cook Range, Middleback Ranges, 21.ix.1981, *N.N. Donner 8015* (AD); 60 km SW of Iron Knob on Kimba road, 16.x.1975, *L. Haegi 706* (NSW, AD, SYD); 15 km ENE of Cowell on Mitchellville road, 26.viii.1977, *L. Haegi 1304* (NSW, AD, BRI, CANB); Between Cowell and Arno Bay, 27.xi.1961, *D.N. Kraehenbuehl 528* (AD); Foot of Iron Duke at eastern end of Middleback Range, 29.xii.1970, *A.E. Orchard 2935* (AD, CANB); c. 6 km W of Plank Point, 2.ii.1977, *L.D. Williams 9025* (AD, NSW); 10 km SE of Wudinna, 18.xi.1984, *D.N. Kraehenbuehl 5051* (AD). **Northern Lofty:** Sections 141–150, Hundred of Wiltunga, 13.ii.1966, *B. Copley 34* (AD); Southern boundary of Section 195, Hundred of Wiltunga, c. 140 km NNW of Adelaide, 20.iii.1966, *B. Copley 144* (AD); Mundoora, c. 50 km SSE of Port Pirie, iv.1962, *G. Gardiner s.n.* (AD96323154); 5.7 km S of Wandearah East Post Office on Port Broughton road, 29.viii.1977, *L. Haegi 1331* (NSW, AD, CORD, K, MEL, MO, PERTH); W of Ninnes, which is 120 km NNW of Adelaide, 8.xii.1963, *D.N. Kraehenbuehl 1049* (AD). **Murray:** Calperum Station, Overflow Track, at a point c. 20 km NNE of Monash, 4.ii.2015, *J.R. Guerin 204* (AD); 20 km NE of Blanchetown on Waikerie road, 5.x.1975, *L. Haegi 676* (NSW, AD, BRI, CBG, NT, PERTH); 18 km WSW of Waikerie on Sturt Hwy to Blanchetown, 15.xi.1975, *L. Haegi 868A–J* [population collection documenting variability] (AD, BRI, CANB, HO, MEL, NSW, NT, PERTH); 16 km N of New Well on road running almost due N to main Blanchetown–Waikerie road, 15.xi.1975, *L. Haegi 869* (NSW, AD); 11 km NNE of Berri, 21.x.1976, *L. Haegi 1252* (NSW, AD); 21 km by road NE of Blanchetown on Waikerie road, 17.xi. 1976, *L. Haegi 1263* (NSW, AD); - also 13.x.1977, *L. Haegi 1457G, H, I, L, M, O, P, Q, R, S, T, U, V, W, X, Y* [population collection at site of occurrence of putative hybrid with *Cyphanthera myosotidea*, also documenting variability in *G. dixonii*] (AD); 2 km NE of Stony Pinch Dam, c. 15 km NW of Renmark, 26.xii.1978, *L. Haegi 1598* (NSW, AD, BIRM, F, HO); Area between Oak Dam (Frenchs Dam) and Gypsum Hills, c. 32 miles (c. 52 km) N of Overland Corner, 9.x.1965, *D.E. Symon 3627* (AD, CANB, K); 45 km NW of Renmark on road to Canopus Station, 27.ii.1976, *L.D. Williams 7768* (AD); Glossop, between Barmera and Berri, x.1963, *Woolmer 75* (AD). **Yorke Peninsula:** 32 km NW of Port Wakefield, 29.iii.1966, *B. Copley 177* (AD); 8 km WNW of Bute, 15.x.1975, *L. Haegi 705* (AD).

Occurrence of putative intergeneric hybrids involving *G. dixonii*

Several specimens not referable to known species were encountered in small areas where populations of *G. dixonii* overlap with those of species in two other genera of Anthocercideae: *Cyphanthera myosotidea* in one case and *Duboisia hopwoodii* in the other. Closer examination reveals that the specimens are visually intermediate between the two sets of parents, suggesting a hybrid origin for these plants. To test this notion further, specimens of the intermediates and parents from each of the two localities were subjected to simple morphometric analysis and an assessment of pollen fertility.

Pollen viability of samples from both putative parents and the morphologically intermediate specimens was tested. A very low rate of staining was recorded in all intermediates, contrasting with high rates in the putative parents and supporting the assessment of the intermediates as of hybrid origin.

Phytochemical investigations of the leaves of the putative parents and hybrids (El Imam *et al.* 1991) provide further evidence for the hybrid origin of the intermediates; these studies revealed that each of the parents has a unique combination of tropane and pyridine alkaloids and that the alkaloid spectra of each set of morphological intermediates combine those found in the parents. Together these various observations provide strong circumstantial evidence for the intermediates being hybrids. The occurrence of intermediates limited to areas of overlap in the distributions of each of the parents is consistent with this conclusion. In both cases, flowering periods overlap. No manipulated crossing experiments have been performed to demonstrate that hybridisation is possible.

Cyphanthera myosotidea × *Grammosolen dixonii*

A few plants visually intermediate between these two species were encountered along the road verge between 20 and 30 km NE of Blanchetown, South Australia, the only area where the two species are known to be sympatric. Their presence followed major disturbance involving extensive earthworks associated with realignment of the road. Here *G. dixonii* was conspicuous and locally common but *C. myosotidea* was rare. A quantitative assessment of these specimens confirms their intermediacy when compared with material of the two species found at the site (Table 1, Fig. 4). Similarly, pollen fertility was low in a specimen

Table 1. Comparison of certain characters in *Cyphanthera myosotidea*, *Grammosolen dixonii* and a putative hybrid.

Character		*Cyphanthera myosotidea*	Putative hybrid	*Grammosolen dixonii*
Indumentum		Inconspicuous, moderately dense pubescence mainly of simple glandular (with a few eglandular) hairs	Moderately conspicuous, moderately dense tomentum of eglandular branched hairs	Conspicuous, dense tomentum of eglandular branched hairs
Leaf	length (mm)	2–10	8–16	8–16
	breadth (mm)	1–4	3–5	6–15
	shape	Ovate to elliptic or narrowly so	Ovate	Ovate-triangular to very broadly so
	length : breadth	(1.8–) 2.0–6.0 (– 8.0)	2.4–3.5	(0.8–) 0.9–1.5 (– 2.5)
	margins	Flat	Slightly undulate	Undulate
Inflorescence		Flowers scattered in distal parts	Flowers in open leafy spikes	Flowers in dense, leafy spikes
Pedicel		Long, conspicuous	± Short, inconspicuous	Short, inconspicuous
Corolla-lobe	shape	Broadly elliptic	Ovate-elliptic	Ovate to elliptic
	length : breadth	0.8–1.3	1.5–1.7	1.4–2.2
Alkaloid spectrum of leaves (after El Imam *et al.* 1991).		Hyoscyamine or atropine; hyoscine (principal alkaloid); norhyoscyamine or noratropine; 6β-hydroxyhyoscyamine; 3α-tigloyloxytropane; scopine or oscine; tropine; 3-phenylacetoxynortropan-6,7-diol.	Hyoscine; apohyoscine; 6β-hydroxyhyoscyamine (principal alkaloid); tropine; two unidentified bases.	Hyoscyamine; hyoscine; apohyoscine; 3α-acetoxytropane; no particular alkaloid recorded as predominant.

Table 2. Pollen sterility estimates in *Cyphanthera myosotidea*, *Grammosolen dixonii* and a putative hybrid.

	Cyphanthera myosotidea	Putative hybrid	*Grammosolen dixonii*
% sterile pollen	2%	61%	2%
No. of grains counted	183	142	121
Voucher specimen	*Haegi 1262*	*Haegi 1265*	*Haegi 1263*

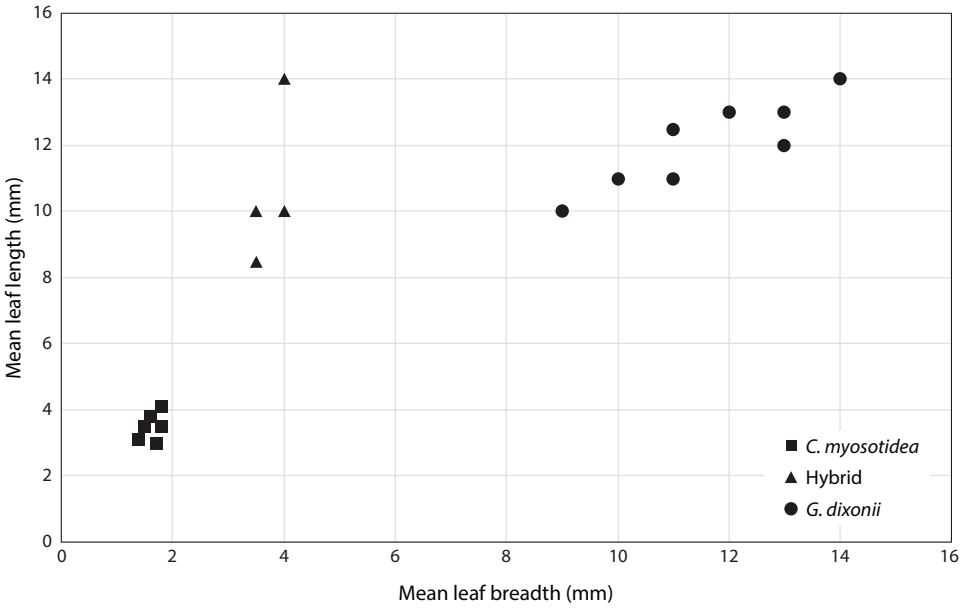

Fig. 4. Scatter plot portraying intermediacy of putative hybrids between *Cyphanthera myosotidea* and *Grammosolen dixonii*, as demonstrated by leaf characters. Each plotted point represents a specimen; four leaves measured per specimen; all specimens from Murray Region, South Australia (cited above and below).

of the intermediate material but high in specimens of the parents from the same site (Table 2). Staining grains in the hybrid were markedly smaller than those of the parents. Observation of meiosis in pollen mother cells of the putative hybrid indicated a high rate of failure in pairing of chromosomes to form bivalents at Metaphase 1, while normal meiosis was observed in the putative parents (see Table 2).

Noting that 6β-hydroxyhyoscyamine, a minor component of *C. myosotidea*, is present as the principal base in the anomalous material and that tropane alkaloid yields of this material are intermediate between those of the two parents, El Imam *et al.* (1991) observe that this is consistent with hybrid origin. They also conclude that hybridisation of these species appears to exert an influence on the capacity of the progeny to convert hyoscyamine into hyoscine, a reaction generally involving 6-hydroxyhyoscyamine as an intermediate.

Specimens seen (all Murray Region, S.A.)

Cyphanthera myosotidea × *Grammosolen dixonii:* c. 13 km S of Waikerie on roadside, 2.ix.1974, *N. Gemmell 293* (AD, MEL); c. 21 km by road NE of Blanchetown bridge on Waikerie road, 17.xi.1976, *L. Haegi 1264 & 1265* (AD); - also 13.x.1977, *L. Haegi 1457A, B, E, J, K, N* [part of population collection, including both parents] (AD); 20 km NE of Blanchetown bridge on Waikerie road, 3.xi.1978, *L. Haegi 1593* (AD); 28 km NE of Blanchetown on Waikerie road, 14.ix.1974, *D.N. Kraehenbuehl 3392* (AD).

Cyphanthera myosotidea: 13 km SSW of Waikerie, 2.ix.1974, *N. Gemmell 297* (AD); c. 21 km by road NE of Blanchetown bridge on Waikerie road, 17.xi.1976, *L. Haegi 1262* (AD); - also 13.x.1977, *L. Haegi 1457C, D, F* [part of population collection, including putative hybrid and both parents] (AD); Waikerie, 15.x.1968, *Miller s.n.* (AD96846176); 61 miles (c. 98 km) SW of Renmark, 18.ix.1967, *B.H.A. Tönnies s.n.* (AD97424250); 16 km WSW of Waikerie, 18.ix.1967, *Wheeler 452* (AD); c. 15 km SW of Waikerie, 26.ix.1971, *D.J.E. Whibley 3618* (AD).

Grammosolen dixonii: see main treatment above.

Duboisia hopwoodii × *Grammosolen dixonii*

Specimens apparently resulting from hybridisation of these species were collected during the 1970's from two sites near Berri and Renmark, c. 200 km NE of Adelaide, South Australia. Both sites have been visited and only a small number of putative hybrids were seen at each. A much more recent collection made in 2015 from a third site in the same area (*Guerin 205*) provides evidence of the intermittent continued recurrence of the hybridisation event. The parents are markedly different from each other in several morphological features (Table 3) and the intermediacy of the hybrid is visually obvious (Figs 2, 5 & 6). The average dimensions of leaves from several specimens collected in the area of occurrence have been plotted to demonstrate this quantitatively (Fig. 7). Pollen from a specimen of putative hybrid origin showed markedly higher sterility than found in either parent (Table 4). A high rate of failure in pairing of chromosomes was observed in pollen mother cells at meiosis, while normal meiosis was observed in the putative parents (see Table 4).

El Imam *et al.* (1991) state that the establishment of nornicotine and hyoscine as the principal alkaloids, together with the co-occurrence of other bases of the parents firmly support the assignment of the intermediate as a hybrid (Table 3).

Specimens of this hybrid were at one time thought to be a new species related to *Cyphanthera albicans* by South Australian botanists. Striking features distinguishing the hybrid from species of the tribe are the glabrescent branches and leaves combined with the undulate margins of the leaves.

Specimens seen

Duboisia hopwoodii × *Grammosolen dixonii:* SOUTH AUSTRALIA. **Murray Region:** 8 km N of Berri, 4.i.1970, *B. Copley 3000* (AD); 8 km N of Berri, 19.xii.1973, *B. Copley 4181* (AD); 11 km NNE of Berri, 21.x.1976, *L. Haegi 1250* (AD); 2 km NE of Stony Pinch Dam, c. 15 km NW of Renmark, 26.xii.1978, *L. Haegi 1600 & 1601* (AD); 2 km NE of Stony Pinch Dam, c. 15 km NW of Renmark, 22.iv.1979, *L. Haegi 1773* (AD); sand ridges 3 km W of Stony Pinch (burnt), 5.x.1980, *A.E. Spooner 7265* (AD); Calperum Station, Overflow Track, at a point c. 20 km NNE of Monash 4.ii.2015, *J.R. Guerin 205* (AD).

Duboisia hopwoodii: SOUTH AUSTRALIA. **Murray Region:** c. 128 m N of Renmark, 6.i.1926, *J.B. Cleland s.n.* (AD966030806); c. 10 km N of Berri, 25.viii.1962, *J.B. Cleland s.n.* (AD97217266); Calperum Station, c. 10 km ENE of Berri, 4.i.1970, *B. Copley 2999* (AD); c. 15 km NE of Monash, 22.iv.1957, *H. Eichler 13823* (AD, CANB); 11 km NNE of Berri, 21.x.1976, *L. Haegi 1251* (AD); Canopus Station, c. 185 km ENE of Burra and c. 95 km N of Renmark, 6.viii.1965, *A.C. Robinson 34* (AD); Calperum Station, Overflow Track, at a point c. 20 km NNE of Monash 4.ii.2015, *J.R. Guerin 203* (AD). NEW SOUTH WALES. **South Far Western Plains:** 110 km S of Broken Hill on Wentworth road, 1.ix.1962, *J.B. Cleland s.n.* (AD97217258).

Grammosolen dixonii: see specimens cited under *G. dixonii* above.

2. *Grammosolen truncatus* (Ising) Haegi

Telopea 2(2) (1981) 178. — *Anthotroche truncata* Ising, *Trans. & Proc. Roy. Soc. S. Austral.* 46 (1922) 605, t. 38, 39, Fig. 1. — **Type citation:** "Ooldea, East-West Railway Line, September 15, 1920, and Barton, in the same district, September 19, 1920." **Lectotype (here designated):** Ooldea, Sept. 1920, *Ising 1297* (AD98209191). **Isolectotypes:** AD, BM, BRI, DNA, CANB, K, L, MEL, NSW. **Remaining syntype:** Barton, 19.ix.1920, *Ising 1374* (AD).

Erect, somewhat stiff, grey-green *shrub* 0.7–2 m tall and diam. *Branches* very densely and closely tomentose with multangulate and multangulate-dendritic hairs mostly 0.1–0.2 mm and fewer to 0.25 mm, the indumentum very gradually wearing with age. *Leaves* mostly ± spreading, some in small clusters on much-condensed

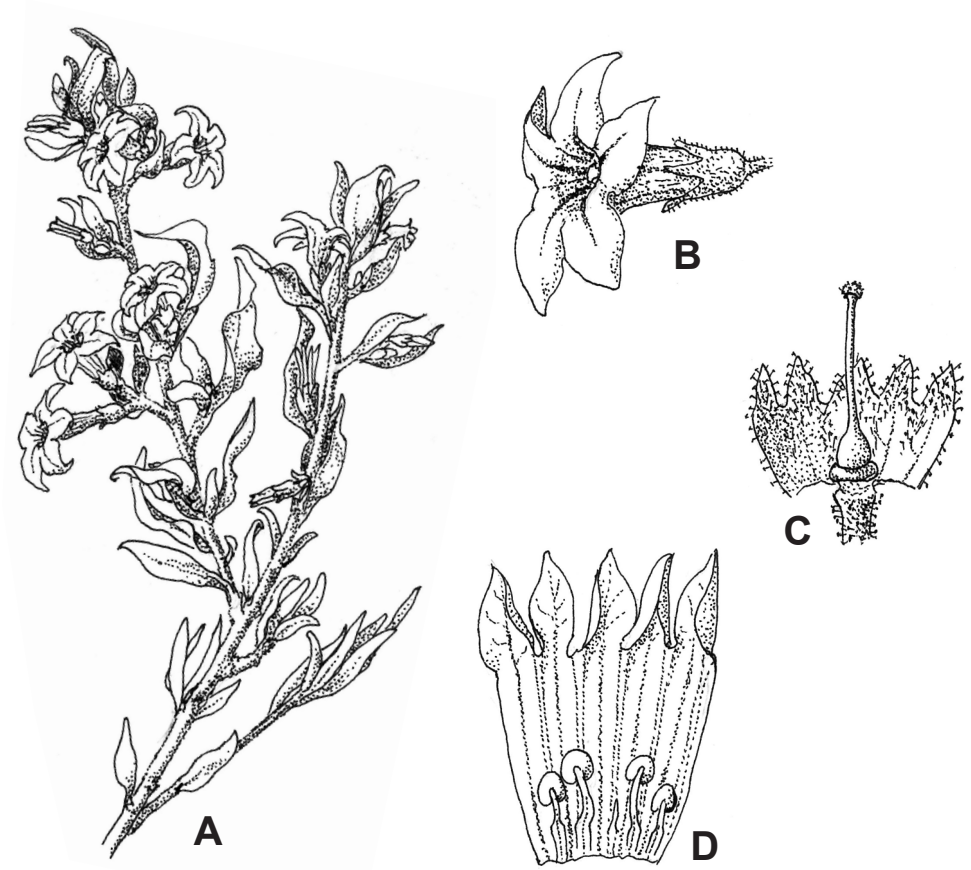

Fig. 5. ***Duboisia hopwoodii*** × ***Grammosolen dixonii.*** **A** flowering branchlet, × 1; **B** flower, × 3; **C** calyx of advanced bud opened out, with pistil, × 5; **D** opened corolla of same, × 5. (*Haegi 1600*). Illustration by M. Perkins.

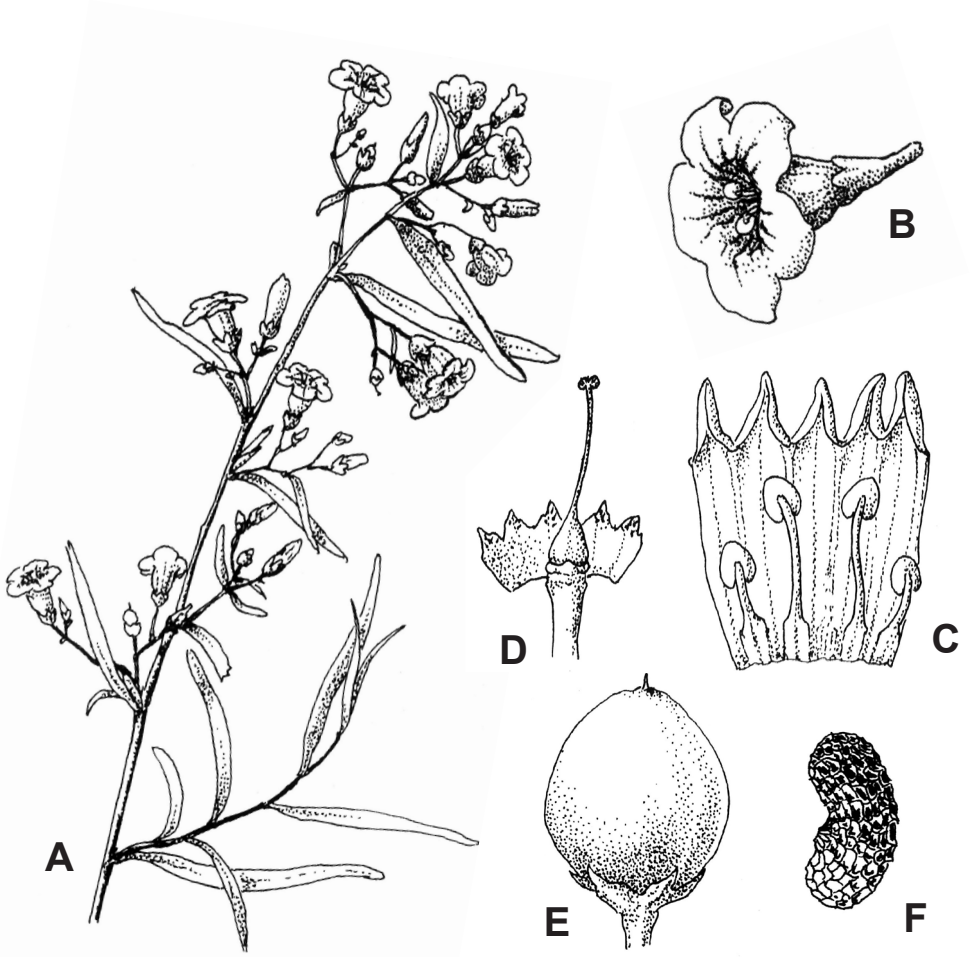

Fig. 6. ***Duboisia hopwoodii.*** **A** flowering branchlet, × 1; **B** flower, × 3; **C** corolla of advanced bud, opened out, × 5; **D** calyx and pistil of same, × 5; **E** berry, × 5; **F** seed, × 10. (*Haegi 888*). Illustration by M. Perkins.

Table 3. Comparison of certain characters in *Duboisia hopwoodii*, *Grammosolen dixonii* and a putative hybrid.

Character		***Duboisia hopwoodii***	**Putative hybrid**	***Grammosolen dixonii***
Indumentum		Glabrous	Immature parts conspicuously tomentose; mature parts glabrescent	Conspicuous, dense tomentum of eglandular branched hairs
Leaf	length (mm)	35–105	8–16	8–16
	breadth (mm)	2–8	3–5	6–15
	length : breadth	(6–) 10–35 (–71)	2.4–4.5	(0.8–) 0.9–1.5 (–2.5)
	margins	Flat	Undulate	Slightly undulate
Corolla-lobe	shape	Broadly ovate to orbicular	Ovate-elliptic	Ovate to elliptic
	length : breadth	(0.3–) 0.5–1.2	1.5–1.7	1.4–2.2
Stamens		4	4 or 5	5
Alkaloid spectrum of leaves (after El Imam *et al.* 1991).		Hyoscine; nicotine; nornicotine (principal alkaloid); N-acetylnornicotine; N-formylnornicotine.	Hyoscine (2nd major alkaloid); apohyoscine and 3α-acetoxytropane in admixture; nicotine (in hyoscine picrate mother liquor); nornicotine (principal alkaloid); N-formylnornicotine.	Hyoscyamine; hyoscine; apohyoscine; 3α-acetoxytropane; no particular alkaloid recorded as predominant.

Table 4. Pollen sterility estimates in *Duboisia hopwoodii*, *Grammosolen dixonii* and a putative hybrid.

	Duboisia hopwoodii	**Putative hybrid**	***Grammosolen dixonii***
% sterile pollen	2.8%	86.0%	1.0%
No. of grains counted	545	372	283
Voucher specimen	*Haegi 1599*	*Haegi 1600*	*Haegi 1598*

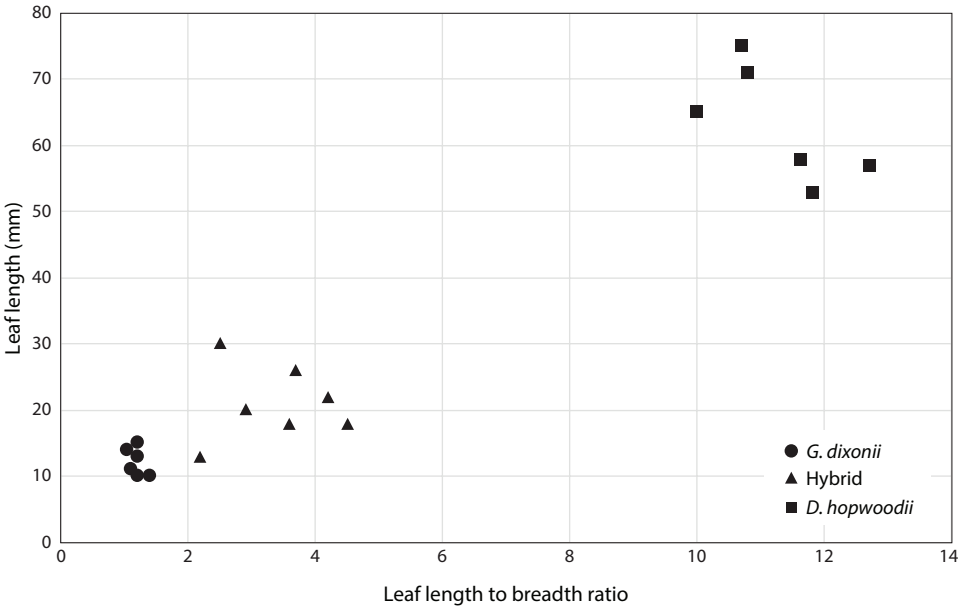

Fig. 7. Scatter plot portraying intermediacy of putative hybrids between *Duboisia hopwoodii* and *Grammosolen dixonii*, as demonstrated by leaf length and leaf length to breadth ratio. Each plotted point represents a specimen; four leaves measured per specimen; all specimens from Murray Region, South Australia or adjacent area in New South Wales (cited above).

axillary branchlets but generally spaced so as not to obscure axis, petiolate; *petiole* 2–4 × 0.5–0.8 mm, tomentose as for lamina; *lamina* ovate to ovate-elliptic, sometimes broadly or narrowly so, less commonly elliptic (L:B 1.1–1.7 (–2.3)), (5–) 7–13 (–18) × (3.5–) 4–10 (–11) mm, very densely and closely tomentose with multangulate and multangulate-dendritic hairs 0.05–0.15 mm above and below; *base* cuneate; *apex* acute to slightly obtuse, blunt; *margin* entire, flat, or often slightly thick or recurved; *midrib* faintly prominent above, prominent, conspicuous and often with visible secondary veins below. *Flowers* borne in short, leafy clusters of one or two, 1–3-flowered cymes on much-condensed lateral branchlets, scarcely aggregated to form leafy spikes; *inflorescence-bracts* 1.5–3 × 0.7–1 mm, moderately tomentose with multangulate-dendritic hairs. *Pedicel* 0.3–0.6 mm, glabrous to moderately pubescent with multangulate-dendritic hairs c. 0.15 mm and glandular hairs 0.1–0.15 mm. *Calyx* 2.5–4 mm, outside very densely tomentose with multangulate-dendritic hairs mostly 0.1–0.2 mm, with fewer c. 0.25 mm, and scattered glandular hairs 0.1–0.15 mm, inside moderately pubescent with antrorse glandular hairs, 0.08–0.15 mm, especially on the lobes; *calyx-lobes* acute to slightly obtuse, angular or blunt, 0.2–0.4 times as long as tube, 0.5–1 × 1–1.2 mm, sinuses obtuse. *Corolla* (7.3–) 9.5–11 mm, ± dull-white with violet striations, outside moderately to densely pubescent with multangulate and forked hairs 0.2–0.25 mm on lobes and upper tube, inside very densely papillose with hairs 0.1–0.2 mm on lobes; *tube* 4.5–6.3 mm, markedly widening in upper 0.5–1 mm, diam. 1.3–1.8 mm at base and 2.8–3.5 mm at limb base; *lobes* elliptic to ovate with truncate base (L:B 1.7–2.4), (2.5–) 3.5–6 × (1.5–) 2.0–2.8 mm, sometimes slightly narrowed at the base, apex rounded to bluntly acute, margin flat. *Stamens* 5, 3–4 mm and 2–3.2 mm; *filament-bases* densely pubescent with simple, forked and sparingly branched hairs, 0.2–0.25 mm, less dense abaxially; *anthers* c. 0.8 × 1.0 mm. *Ovary* globose to depressed globose, 0.8–1 × 0.8–1.1 mm; *ovules* 5–10 in total; *style* 2.9–4 mm, ± equal to the longer stamens and included by 0.5–1 mm; *disc* undulate, 0.3–0.5 mm high, usually slightly, rarely much greater in diameter than ovary (to 1.5 mm), red. *Capsule* somewhat inconspicuous, partly embedded in hairs of enclosing calyx, axis and leaves, globose, 4–4.5 mm diam. *Seeds* c. 4, c. 2.8 × 1.2 mm; *surface-reticulae* 0.1–0.25 × 0.1–0.25 mm. *Chromosome number:* n=56 (*Haegi 1597*). **Fig. 8.**

Distribution and Ecology. *Grammosolen truncatus* occurs in South Australia and Western Australia, extending from north-west Eyre Peninsula and the western Gawler Ranges north-west into the southern Great Victoria Desert. It is always found on deep sandy soils, commonly on sand dunes or localised sandy rises. It is primarily a plant of burnt or otherwise disturbed sites in mallee vegetation, sometimes associated with *Callitris* and seems to occur mainly in small scattered populations. See *G. dixonii* above for comments on the co-occurrence of these two species on Eyre Peninsula (Fig. 3).

Phenology. Flowering specimens have been collected from August through February but the main flowering season appears to be in September and October. Fruiting specimens have been collected in September, October and January. Data are unavailable for the months March to July.

Conservation status. *Grammosolen truncatus* is an uncommon plant known from only about 70 collections. It is not recorded from any conservation reserves.

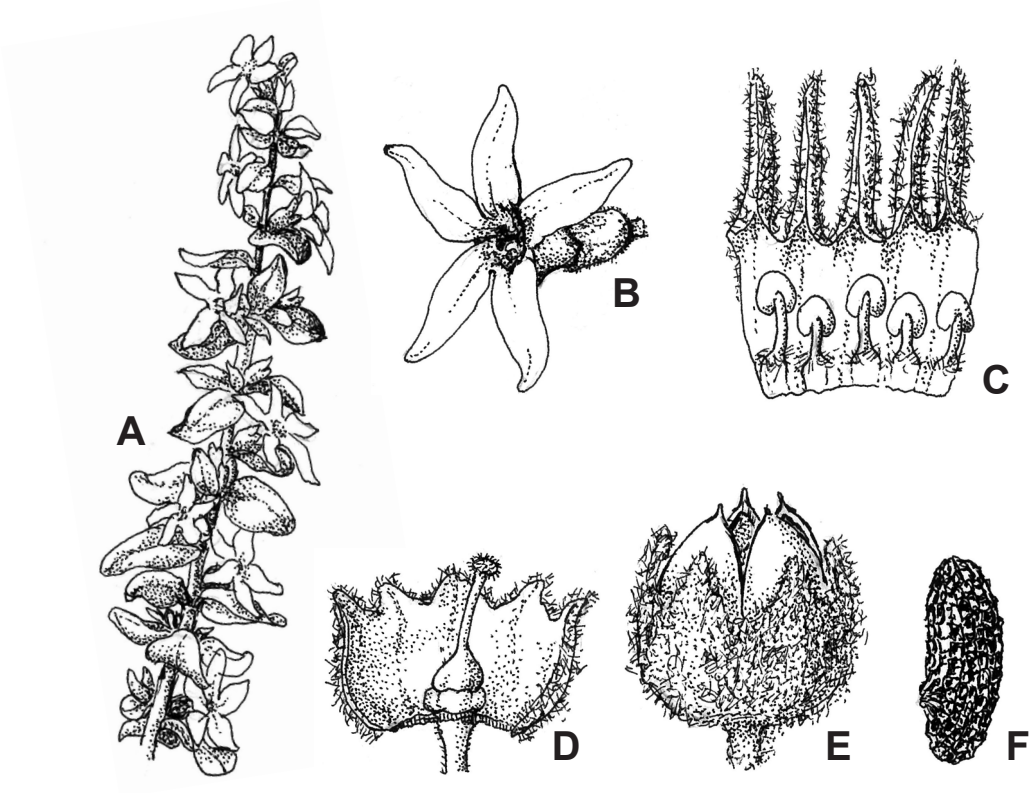

Fig. 8. *Grammosolen truncatus.* **A** flowering branchlet, × 1; **B** flower, × 2.5; **C** corolla of advanced bud, opened out, × 6; **D** opened calyx and pistil of same, × 6; **E** capsule, × 6; **F** seed, × 10. (*Haegi 770*). Illustration by M. Perkins.

Diagnostic features. *Grammosolen truncatus* is clearly related to *G. dixonii* and *G. archeri* but is perhaps closer to *G. archeri*. The western extremity of the range of *G. dixonii* almost meets but does not overlap with the eastern extent of the occurrence of *G. truncatus*, while *G. archeri* has a distinct geographical range separated by several hundred kilometres from both other species.

Variation. *Grammosolen truncatus* is relatively uniform throughout its range, with both the smallest-leaved specimens (e.g. *Symon 8120*, *Blaylock 2035*) and the largest-leaved ones (e.g. *Haegi 770*) occurring in the Gawler Ranges populations.

Hybrids. None recorded.

Derivation of name. From the Latin *truncatus*, truncate, in reference to the shortly lobed calyx, as indicated in the protologue.

Notes. Some details in the protologue description have not been substantiated in this study. My observations indicate that the hairs of the indumentum are not "plumose" but multangulate-dendritic; the stamens are included, not "scarcely exsert" and the ovary is glabrous, not "with a few stellate hairs". Examination of the greater number of specimens now available indicates that up to four seeds develop: in Ising's material the capsules were one-seeded.

Selected specimens (70 examined)

WESTERN AUSTRALIA. **Great Victoria Desert IBRA Region:** Anne Beadell Highway, 37 km E by track of Ilkurkla roadhouse, 6.x.2010, *R. Davis, J. Jackson & D. Ferguson 11636* (PERTH, CANB *n.v.*). SOUTH AUSTRALIA. **North Western:** c. 135 km N of Cook, just in main dunes, 18.viii.1980, *D.E. Symon 12233* (AD, NSW). **Nullarbor:** 2 miles [c. 3 km] S of Maralinga on sand ridge, 10.x.1956, *N. Forde 620* (AD, CANB); 35 km E of Barton on Transcontinental Railway, 24.x.1970, *B. Lay 81* (AD, MEL). **Gairdner Torrens:** 15 km S of Lake Everard Homestead, 20.ix.1972, *J.Z. Weber 3202* (AD). **Eyre Peninsula:** 30 km NW of Ceduna, 2 km NW of Koonibba Hill, 4.i.1979, *M.D. Crisp 4756* (CBG, AD, NSW); 60 km NNE of Minnipa on Yardea road, 18.x.1975, *L. Haegi 770* (AD, CBG, NSW); 17 km SSW of Hiltaba on Yantanabie road, 19.x.1975, *L. Haegi 775* (AD, BIRM, BRI); 20 km N of Karcultaby, 20.x.1975, *L. Haegi 794* (AD, CORD, MO); c. 29 km by road SW of Yardea Homestead on Minnipa road, 29.x.1978, *L. Haegi 1597* (NSW, AD, CANB, F, HO); 12.4 km directly SSE of Mt. Stuart, 11.x.1999, *D.E. Murfet & R. Taplin 19991011* (AD); 2.9 km directly SSW of Corabinnie Hill, 19.x.2001, *S.D. Kenny BS 128-276* (AD168685).

3. *Grammosolen archeri* Haegi, *sp. nov.*

Grammosolen sp. Mt Ridley (*W.R. Archer 1210911*) W. Austral. Herb., *FloraBase—the Western Australian Flora* (1998–), https://florabase.dpaw.wa.gov.au/ [accessed 5 June 2019]; CHAH, *Austral. Pl. Cens.* (2006), https://biodiversity.org.au/nsl/services [accessed 5 June 2019]. — **Holotype:** Western Australia, Eastern Mallee IBRA subregion, [Vicinity of] Lake Halbert [precise locality details withheld for conservation reasons], 8 Oct. 1990, *W.R. Archer 510907* (PERTH). **Isotypes:** AD, BM, CANB, MEL, MO, to be distributed.

Spreading grey-green *shrub*, 0.6–1 m tall and up to 2 m diam. *Branches* very densely and closely tomentose with multangulate and multangulate-dendritic hairs, mostly c. 0.2 mm and fewer to 0.25 mm, the indumentum gradually wearing off with age. *Leaves* mostly ± spreading, some at times in small clusters on much condensed axillary branchlets but generally spaced so as not to obscure the axis, petiolate; *petiole* 0.4–2.2 × 0.4–0.7 mm, tomentose as for lamina; *lamina* orbicular-reniform to obcordate, sometimes broadly ovate at the shoot tips (L:B 0.65–0.96 (–1.1)), 2.5–7 × 2.6–10 mm, very densely and closely tomentose with multangulate and stalked multangulate-dendritic hairs, 0.1–0.15 mm above and below; *base* usually truncate or shallowly cordate, sometimes broadly cuneate; *apex* bluntly obtuse to rounded; *margin* flat, sometimes thick or slightly recurved; *midrib* obscure adaxially, ± prominent abaxially, sometimes with secondary veins. *Flowers* borne in 1–2-flowered cymes in the distal leaf axils of short or elongate branchlets, scarcely aggregated to form leafy spikes; *inflorescence-bracts* 0.4–0.6 × 0.1–0.2 mm, densely tomentose with multangulate-dendritic hairs. *Pedicel* 0.3–0.5 mm, pubescent with multangulate-dendritic hairs c. 0.15 mm, glandular hairs absent. *Calyx* 2.0–2.5 mm, outside very densely tomentose with multangulate-dendritic hairs mostly 0.1–0.2 mm and fewer to 0.25 mm, inside moderately pubescent with antrorse glandular hairs 0.06–0.1 mm, especially on the lobes; *calyx-lobes* acute, blunt, 0.4–0.5 times as long as tube, 1 × 0.8 mm, sinuses acute. *Corolla* 5.5–6 mm, dull white, striations not recorded, outside moderately to densely pubescent with multangulate and forked hairs 0.15–0.25 mm on the lobes and upper tube, inside very densely papillose with hairs 0.08–0.1 mm on lobes; *tube* 3.5–4 mm long, markedly widened in upper 0.5 mm, diam. 1.2–1.4 mm at base, and 2.0–2.4 mm at limb-base; *lobes* ovate-elliptic with truncate base, (L:B 1.7–1.8), 2.0–2.5 × 1.2–1.4 mm, sometimes slightly narrowed at base, apex rounded to bluntly obtuse, margin flat. *Stamens* 5, the longer ones 3.0–3.3 mm and the shorter ones 2.5–2.7 mm; *filament-bases* densely pubescent with simple, forked and sparingly-branched eglandular hairs 0.2–0.3 mm, equally dense abaxially; *upper anthers* c. 0.5 × 0.6 mm, *lower anthers* sometimes slightly smaller, 0.4–0.5 × 0.5–0.6 mm. *Ovary* globose, 0.6 mm diam.; *ovules* 6–8 in total; *style* 1.9–2.1 mm, ± equal to the longer stamens and included by 0.5 mm; *stigma* c. 0.15 × 0.3 mm; *disc* undulate, 0.2–0.3 mm high, c. 0.8 mm diam., colour and consistency unknown. *Capsule* ± inconspicuous, largely enclosed by the tomentose calyx, globose, 2.5–3.0 mm diam. *Seeds* 3–4, c. 2.2 × 1.2 mm; surface-reticulae 0.1–0.15 × 0.05–0.15 mm. *Chromosome number* not determined. **Fig. 9.**

Distribution and Ecology. Endemic to Western Australia where it is to date known only from the Eastern Mallee IBRA subregion in the South Western Province, in an area 70–90 km inland from the coast between Esperance and Cape Arid. The three known

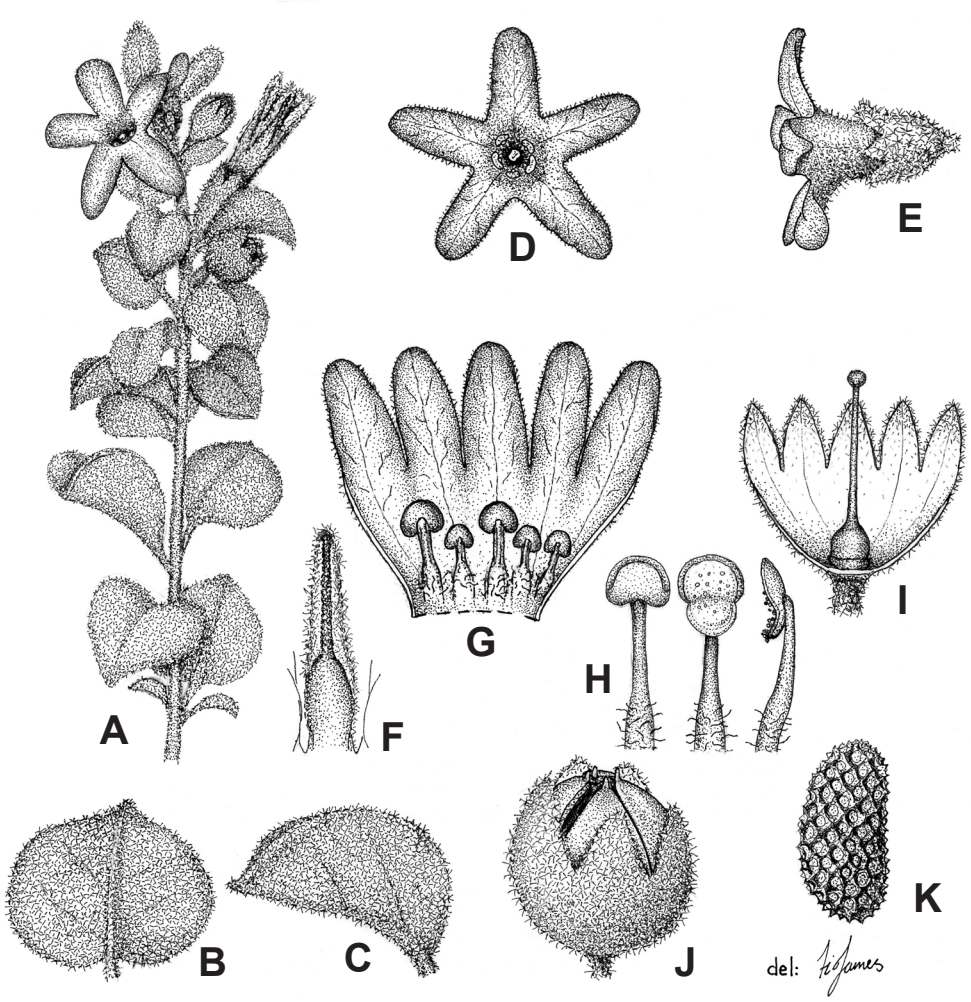

Fig. 9. ***Grammosolen archeri.*** **A** flowering branchlet, × 4.5; **B** leaf, spread, upper side, × 7.5; **C** leaf showing orientation and underside, × 7.5; **D** flower from above, × 6; **E** flower from side, × 6; **F** corolla lobe, late bud stage, × 12; **G** corolla opened out, with androecium, × 7.5; **H** stamens showing adaxial dehiscence, × 19; **I** calyx opened out, with pistil, × 9; **J** capsule, × 7.5; **K** seed, × 11. (*W.R. Archer 2909916*). Illustration by F. James.

populations occur below 200 m altitude in the 300 mm to 400 mm mean annual rainfall zone, on disturbed sites in deep sandy loam soil and in mallee-heath vegetation (Fig. 3).

Conservation status. Rare and poorly known. Listed under the schedules of the Western Australian Wildlife Conservation (Rare Flora) Notice as a Priority 1 species, reflecting inadequate knowledge of its occurrence and abundance, because of the small number of collections and relatively poorly collected area it occurs in.

Diagnostic features. *Grammosolen archeri* differs from all three other species in its distinctive, small, orbicular-reniform to obcordate leaves and in its much smaller flowers and fruits. It seems closest to *G. truncatus* and, perhaps somewhat less so, to *G. dixonii*. It is of similar appearance, with a dense covering of multangulate and multangulate-dendritic hairs on vegetative parts and with flowers of very similar appearance (dull white corolla with ovate-elliptic lobes; the occurrence of striations in the tube is expected but yet to be observed). Like *G. dixonii* it has a spreading habit and subsessile leaves, while it is similar to *G. truncatus* in being more openly branched and having small inflorescences borne on short lateral shoots (though these are sometimes elongate in *G. archeri*). In *G. dixonii* the leaves are usually closely spaced so as to be overlapping, concealing the axis (especially in the more distal parts), and with flowers aggregated into leafy spikes. From *G. odgersii* it differs in having five (cf. four) fertile stamens and in lacking verticillately-branched hairs on the vegetative parts.

Variation. No appreciable patterns of variation are evident in *G. archeri*, which is recorded from only three collections across an area about 100 × 20 km.

Derivation of name. Named for William R. Archer, botanical collector and horticulturist of Esperance, Western Australia, who first discovered this species in the field and has collected the only known material of it.

Specimens seen (precise locality details withheld for conservation reasons)

WESTERN AUSTRALIA. **Eastern Mallee IBRA subregion:** [Vicinity of] Lake Halbert, 17 Feb. 1990, *W. Archer 1702903* (AD; PERTH, to be distributed); 12.x.1991, *W.R. Archer 1210911* (MEL; also PERTH, HO *n.v.*); [Vicinity of] Mt Ridley, 13.x.1990, *W.R. Archer 13109010* (AD; PERTH, BRI, BM, to be distributed); [Vicinity of] Mt Buraminya, 29.ix.1991, *W.R. Archer 2909916* (AD; CANB, MEL *n.v.*; K, NSW, PERTH, to be distributed).

4. *Grammosolen odgersii* (F.Muell.) Haegi, *comb. nov.*
Anthocercis odgersii F.Muell., *Fragm.* 10 (1876) 19; C.A.Gardner, *Enum. Pl. Austral. Occ.*, Part 3 (1931) 116; Beard, *Descr. Cat. W. Austral. Pl.* (1965) 95; J.W.Green, *Cens. Vasc. Pl. W. Austral.* (1981) 92. — *Cyphanthera odgersii* (F.Muell.) Haegi, *Telopea* 2 (1981) 177; R.W.Purdie, Symon & Haegi, *Fl. Austral.* 29 (1982) 27. — **Type citation:** "Ad fontes Victoriae; Young". **Lectotype (here designated):** Victoria Spring [Queen Victoria Spring, Western Australia, 30°26'S 123°24'E], *s.dat.*, *Young s.n.* (MEL70945). **Isolectotype:** MEL70234.

Grey-green soft *shrub* 0.5–2.5 m high with ascending or radiating, often arched branches. *Branches* very densely lanate-tomentose with verticillately branched eglandular hairs 0.3–6.5 mm long and scattered simple glandular hairs 0.25–0.5 mm. *Leaves* ± scattered or often crowded towards the ends of branches, spreading, subsessile; *lamina* broadly to narrowly ovate-elliptic (L:B 1.1–3.8), (11–) 12–30 (–35) × 7–13 mm, very densely lanate-tomentose above and below with verticillately branched hairs 0.3–1.0 mm; *base* cuneate to attenuate; *apex* acute and blunt to obtuse or rounded; *margin* flat, rarely slightly inrolled or undulate; *midrib* obscure above and below. *Flowers* in dense axillary and terminal clusters, often forming leafy spikes; *upper inflorescence-bracts* to 5 mm, narrowly elliptic, moderately pubescent adaxially with oblique to antrorse glandular hairs 0.05–0.25 mm, and densely lanate-tomentose abaxially (and also near the apex adaxially) with verticillately branched hairs 0.5–2 mm. *Pedicel* 0.5–2 mm, sparsely to moderately pubescent with simple glandular hairs 0.05–0.75 mm. *Calyx* 4–7 mm, pubescent outside in lower half as for pedicel, in upper half very densely lanate-tomentose with porrect to oblique verticillately branched hairs 0.5–2.5 mm, often entirely obscuring calyx, pubescent inside with porrect to antrorse glandular hairs 0.05–0.25 mm; *calyx-lobes* 2–3 × 1.0–1.7 mm, acute to acuminate, blunt, sinuses acute, angular. *Corolla* 5.5–8.5 mm, white with violet striations, sparsely pubescent outside with glandular hairs 0.05–0.2 mm, very densely pubescent inside with papillae 0.05–0.1 mm; *tube* 4.2–6.5 mm, diam. 0.8–1.5 mm at base and 2.5–4 mm at limb base; *lobes* ovate to broadly ovate with truncate base (L:B 1.1–2.3), 1.3–2.5 × 1.1–1.6 mm, fused for 0.5–1 mm at base, apex rounded, margin flat but whole lobe often somewhat concave. *Stamens* 4, the upper ones 2.0–3.0 mm and the lower ones 1.3–2.2 mm; *filament-bases* pubescent with simple and forked or dendritic eglandular hairs 0.1–0.5 mm and sometimes glandular hairs 0.05–0.15 mm; *anthers* c. 0.8 × 1 mm. *Ovary* ovoid, 0.6–1.6 × 0.5–1.2 mm; *ovules* 5–6 in total; style 2.5–3 mm; *stigma* 0.2–0.3 × 0.3–0.4 mm; disc even to slightly undulate, 0.1–0.3 mm high, bright red. *Capsule* inconspicuous, embedded in dense, long hairs of calyx and axis, ellipsoid to ovoid or broadly so, 3–5 × 2–4 mm. *Seeds* 1–4, 2.8–3.4 × 1.1–1.4 mm; *surface reticulae* 0.2–0.4 × 0.2–0.3 mm. *Gametic chromosome number:* n=30 (*Chinnock 3100*). **Figs 10 & 11.**

Distribution and Ecology. *Grammosolen odgersii* is endemic to southern inland Western Australia where it occurs in a few widely scattered populations in the Avon Wheatbelt and Coolgardie IBRA regions. The range falls entirely within the 150 mm to 500 mm mean annual rainfall zone (Fig. 3).

Conservation Status. See subspecies below.

Diagnostic features. *Grammosolen odgersii* is readily distinguishable from all the other three species in the genus in having flowers with only four (not five) fertile stamens, and in the indumentum on the vegetative parts consisting of very long verticillately branched hairs, up to 6.5 mm long on the axes and up to 1 mm long on the leaves (cf. multangulate and multangulate-dendritic hairs no more than 0.25 mm long in *G. truncatus* and *G. archeri* and a mixture of multangulate-dendritic and verticillately branched hairs no more than 1.5 mm long in *G. dixonii*). *Grammosolen odgersii* is perhaps closest to *G. dixonii* but differs further from it in leaf-shape: broadly to narrowly ovate-elliptic (L:B 1.1–3.8), cf. ovate-triangular to very broadly so, sometimes subcordate (L:B (0.8–) 0.9–1.5 (–2.5)) in *G. dixonii*.

Variation. Although *G. odgersii* is known from fewer than 30 collections, a geographically correlated, bimodal pattern of variation is evident, based on several characters (Table 5). Plants from four populations at the western end of the distribution differ from all other populations mainly in having longer, proportionally narrower leaves, a longer indumentum and shorter corolla-lobes. These have been recognised as subsp. *occidentalis* (Haegi 1981). There are no overlaps in the distributions of the two subspecies and although subsp. *odgersii* has a wide east-west occurrence, there is no perceptible gradation towards subsp. *occidentalis*.

Derivation of name. Named in honour of William Henry Odgers (1828–1881), an under-secretary of the Victorian Chief Secretary's Department, who supported Ferdinand von Mueller (the author of the name) in his cause of carrying out botanical research as an officer of the Victorian Government (see protologue, cited above; Sharr 1978).

Vernacular name. Woolly anthocercis (Grieve & Blackall 1975); woolly cyphanthera (Canackle & Moore 2014).

Key to subspecies of *G. odgersii*

1. Leaves with L:B of 1.1–2.0 and 20 mm or less in length; corolla lobes 2.0–2.5 mm . . . . . **4a.** subsp. ***odgersii***

1: Leaves with L:B of 2.3–3.8 and 18–35 mm in length; corolla lobes 1.3–1.8 mm. . . .**4b.** subsp. ***occidentalis***

Table 5. Morphological differences between the two subspecies of *G. odgersii*.

Character	subsp. *odgersii*	subsp. *occidentalis*
Habit	Low shrub 0.5–1m	Shrub 1–2.5 m
Length of indumentum	0.2–2.0 mm	0.5–3.0 mm
Length to breadth ratio of leaves	(1.1–) 1.4–1.8 (–2.0)	(2.3–) 2.5–3.3 (–3.8)
Leaf length	11–20 mm	18–35 mm
Pedicel length	0.5–1.5 mm	0.9–2.0 mm
Corolla-lobe length	2.0–2.5 mm	1.3–1.8 mm
Pubescence at filament bases	Simple glandular and eglandular hairs	Simple and dendritic eglandular hairs

4a. *Grammosolen odgersii* subsp. *odgersii*

Anthocercis odgersii F.Muell.: F.Muell., *Syst. Cens. Austral. Pl.* (1882) 96; F.Muell., *Second Syst. Census. Austral. Pl.* (1889) 163 (where distribution given erroneously as Northern Australia ("N.A."); Ewart, *Vict. Naturalist* 23(9) (1907) 155, p.p. excluding Cowcowing material; Ewart, *Vict. Naturalist* 24(1) (1907) 12–13, p.p. excluding Koch specimen; Ewart, *Vict. Naturalist* 24(6) (1907) 56, p.p. as to Victoria Springs material; B.J.Grieve & W.E.Blackall, *How to Know W.A. Wildfl.* 4 (1975) 610, [110], p.p., as to "Leaves orbicular-ovate" and ref. to Coolgardie District.

Cyphanthera odgersii (F.Muell.) Haegi subsp. *odgersii*, *Telopea* 2 (1981) 177.

Chloanthes drummondii R.Helms ex Ewart, *Vict. Naturalist* 24 (1907) 12, as '*drummondi*', *nom. inval.*

Shrub 0.5–1 m high with radiating often arched branches. *Branch-indumentum* 0.3–2.0 mm. *Leaf-lamina* ovate-elliptic to broadly so (L:B 1.3–2.2), 11–20 × 7–11 mm, with indumentum 0.3–0.9 mm. *Corolla-lobes* ovate to broadly ovate (L:B 1.3–2.3), 2.0–2.5 × 1.0–1.5 mm. *Filament-bases* pubescent with simple eglandular and glandular hairs. *Gametic chromosome number* n=30 (*Chinnock 3100*). **Fig. 10.**

Distribution and ecology. Subspecies *odgersii* occurs in Western Australia over a wide area from the far western Great Victoria Desert westwards to near Southern Cross, in the 150 mm to 500 mm rainfall zone. It is a rarely encountered plant which occurs in widely scattered populations on open sites in mallee, on sand dunes and sandplain, often following fire. Flowering has been recorded from August to October and fruiting in September and October (Fig. 3).

Conservation status. Uncommon to rare but not threatened.

Variation. Little variation is evident among the small number of specimens of this species collected.

Specimens seen (all cited)

WESTERN AUSTRALIA. **Coolgardie IBRA Region:** Victoria Desert, Camp 58, Elder Exploring Expedition, 25 km NE of Streich Mound, 21.ix.1891, *R. Helms s.n.* (AD96414102, AD97604848, MEL70235, MEL70946, NSW123728, NSW123729); 35 km W of Plumridge Lakes, 8.5 km WNW of Salt Creek airstrip, 15.ix.1979, *J. Taylor 498, M. Crisp & R. Jackson* (CBG, NSW); 89.9 km WSW of Coolgardie, just E of Boorabbin, 18.ix.1976, *R.J. Chinnock 3098, 3099 & 3100* (AD); 82.8 km WSW of Coolgardie, near Boondi, 18.viii.1977, *R.J. Chinnock 3674* (AD); 20.5 km E of Zanthus along Transcontinental Railway line, 17.ix.1979, *M.D. Crisp 5881, J. Taylor & R. Jackson* (PERTH; CBG, NSW *n.v.*); c. 90 km by road SW of Coolgardie on Great Eastern Highway, 4.vii.1979, *L. Haegi 1780* (NSW, BRI, F, PERTH); Near Warangering, Camp 81, Elder Exploring Expedition, 14.xi.1891, *R. Helms s.n.* (AD96414101, AD96430080, MEL70236); Goddard (now Ponton) Creek E of Zanthus, 3.x.1956, *R.D. Royce 5570* (PERTH); 20 km E of Zanthus, 2.ix.1968, *P.G. Wilson 7629* (PERTH, AD); 20.5 km E of Zanthus at Goddard (now Ponton) Creek, 9.xi.1976, *E. Wittwer 1977* (PERTH).

4b. *Grammosolen odgersii* subsp. *occidentalis* (Haegi) Haegi, comb. nov.

Cyphanthera odgersii (F.Muell.) Haegi subsp. *occidentalis* Haegi, *Telopea* 2 (1981) 178; R.W.Purdie, Symon & Haegi, *Fl. Austral.* 29 (1982) 28. — **Type:** "Western Australia, Avon District" [precise locality details withheld for conservation reasons], 23.ix.1976, *L. Haegi 1100*. **Holotype:** PERTH. **Isotypes:** AD, CANB, K, MO.

Anthocercis odgersii F.Muell.: Ewart, *Vict. Naturalist* 23(9) (1907) 155, p.p. as to Cowcowing material; Ewart, *Vict. Naturalist* 24(1) (1907) 12–13, p.p. as to Koch specimen; Ewart, *Vict. Naturalist* 24(6) (1907) 56, p.p. as to Koch specimen; B.J.Grieve & W.E.Blackall, *How to know W.A. Wildfl.* 4 (1975) 610, [110], p.p. as to "linear-oblong", illustration and reference to Avon District.

Erect *shrub* 1–2.5 m high with ascending branches. *Branch indumentum* 1.0–6.5 mm. *Leaf-lamina* ovate-elliptic to narrowly so (L:B 2.3–3.8), 18–35 ×

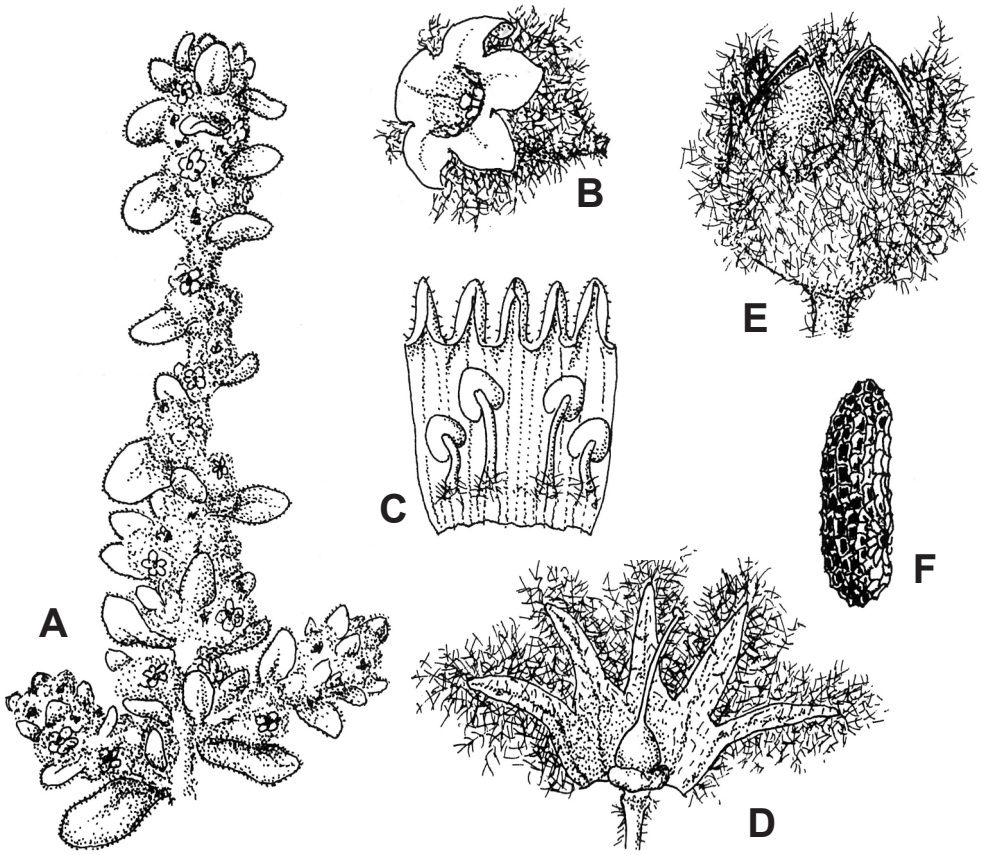

Fig. 10. *Grammosolen odgersii* subsp. *odgersii*. **A** flowering branchlet, × 1; **B** flower, × 3; **C** corolla of advanced bud opened out, × 5; **D** opened calyx and pistil of same, × 5; **E** capsule, × 5; **F** seed, × 10. (*Chinnock 3100*). Illustration by M. Perkins.

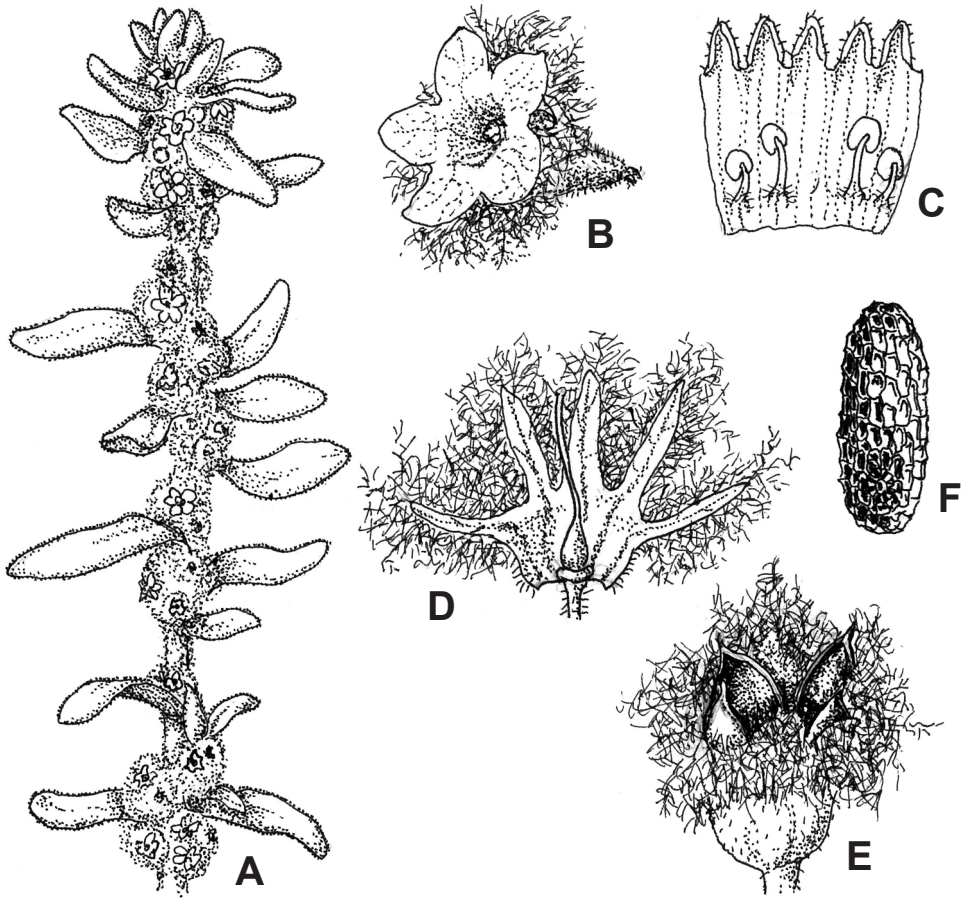

Fig. 11. *Grammosolen odgersii* subsp. *occidentalis*. **A** flowering branchlet, × 1; **B** flower, × 4; **C** corolla of advanced bud opened out, × 5; **D** opened calyx and pistil of same, × 5; **E** capsule, × 5; **F** seed, × 10. (*Haegi 1100*). Illustration by M. Perkins.

8–13 mm, with indumentum 0.5–1.0 mm. *Corolla-lobes* broadly ovate (L:B 1.1–1.5), 1.3–1.8 × 1.0–1.6 mm. *Filament-bases* pubescent with eglandular hairs only. *Chromosome number* not determined. **Fig. 11.**

Distribution and ecology. *Grammosolen odgersii* subsp. *occidentalis* is known from a few small, scattered populations in the Avon Wheatbelt and adjacent Coolgardie IBRA regions in Western Australia, in association with salt lakes forming parts of ancient shallow drainage systems. Plants occur in deep sandy to sandy loam soils, often on disturbed sites (e.g. following fire) in mallee/woodland (Fig. 3).

Conservation status. Listed in Western Australia, (as *Cyphanthera odgersii* subsp. *occidentalis*), applying international criteria, as *Critically Endangered*. For this reason only generalised locality information is provided here. *Grammosolen odgersii* subsp. *occidentalis* has been the subject of intensive recovery work protecting existing populations, propagation of plants for translocation and collection of seed for long-term germplasm storage (Canackle & Moore 2014).

Variation. Little variation is evident among the small number of specimens of this species collected.

Specimens seen (all cited — precise locality details withheld for conservation reasons)

WESTERN AUSTRALIA. **Avon Wheatbelt IBRA Region:** Sep. 1904, *M. Koch s.n.* (no. 1104) (AD, K, MEL70237, MEL70238, MEL70944, NSW, PERTH); Oct. 1939, *C. Gardner s.n.* (PERTH); 3.xii.1946, *C. Gardner 8507* (PERTH); 19.x.1990, *F.H. & M.P. Mollemans 3470* (PERTH); 28.x.1997, *J.A. Cochrane 2460* (PERTH); 12.ix.2007, *J.M. Collins 280* (PERTH); 12.ix.2007, *L. Duffy LD140* (PERTH). **Coolgardie IBRA Region:** June 1990, *F.H. & M.P. Mollemans 2981* (AD, PERTH); 13.ix.1990, *F.H. & M.P. Mollemans 3114* (AD, PERTH).

Acknowledgements

The study described here commenced while the author was employed at the Waite Agricultural Research institute, University of Adelaide during 1976 and 1977 and a PhD student at Flinders University of South Australia (1977–1983). The work continued at the National Herbarium of New South Wales (1977–1982) and then at the Botanic Gardens of Adelaide (from 1982). During this time it was supported by grants from the Australian Biological Resources Study, for which I record my gratitude. After a considerable dormancy the work recently recommenced in Adelaide and I thank the Board of the Botanic Gardens and State Herbarium of South Australia for this opportunity, made possible by the support I receive as an Honorary Research Associate. My thanks go to my colleagues at all the institutions mentioned including my PhD supervisor Bryan Barlow, but in particular the late David Symon, not only a supervisor but also a mentor and wise friend. Jim Armstrong, the late Don McGillivray and Jocelyn Powell (Sydney), Philip Short (Melbourne) and Bob Chinnock, Bill Barker, Robyn Barker and Ed Biffin (Adelaide) are sincerely thanked for their beneficial discussions and in some cases assistance in the field. Likewise, I acknowledge provision of several helpful suggestions by an anonymous referee – these have been incorporated in an amended version of the paper. Kathy Stephens and Marie Taylor (Sydney) provided excellent technical assistance; Margaret Perkins and Rob Roden prepared most of the drawings while temporarily employed at the National Herbarium of New South Wales. Fiona James, as a student in botanical illustration at the State Herbarium of South Australia, prepared the excellent plate of *Grammosolen archeri*. My thanks go to Bill Barker for preparing the distribution map using QGIS and useful GIS layers with point data I provided from the ALA download. My deep gratitude goes to my wife Rosalie Haegi for her support, encouragement and unstinting help throughout the life of the project, not least in assisting with fieldwork.

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