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Taxonomy of the Genus Phymaspermum (Asteraceae, Anthemideae)

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Abstract—Phymaspermum, the largest and most complex genus within the subtribe Phymasperminae, is revised and 17 species are recognised, all endemic to southern Africa. Four new species are described (P. aphylllum, P. comptonii, P. oppositifolium, and P. trisatum), five species are reduced into synonymy (P. bolusii, P. equisetoides, P. montanum, P. pubescens, and P. villosum) and P. thyridaeoides is recognised as the oldest available epithet for P. schroeteri. The species of Phymaspermum can be distinguished by a combination of habit, leaf, involucral, and fruit characters. Species relationships are assessed in a cladistic analysis of 12 anatomical and morphological characters. Phymaspermum is distinguished from Eumorpha and Gymnopentzia by the unique stalked myxogenic trichomes on the fruit surface. This character is shown to be a synapomorphy for Phymaspermum although subsequently lost in two species and replaced by resin canals in the fruit ribs. A comprehensive taxonomic treatment is presented, including a key to the species, correct nomenclature, typification, descriptions, and geographical distributions.

Keywords—Cladistic analysis, Eumorpha, fruit anatomy, Gymnopentzia, morphology, myxogenic trichomes, new species.

Phymaspermum Less. is the largest genus within the subtribe Phymasperminae with 18 species previously recognised, all endemic to southern Africa (Germishuizen et al. 2006). The genus was described by Lessing (1832) for a single species (P. juncceum) and later expanded by Källersjö (1986) to include species which had previously been placed within other genera such as Athanasia L., Brachymeris DC., and Pentzia Thunb. Several of the species are now grazed by livestock (Shearing and Van Heerden 1994; Vlok and Schutte-Vlok 2010; Schutte-Vlok pers. comm.). In particular, the vernacular name of P. parvifolium, “good karoo,” alludes to its importance as a pasture plant for Merino sheep (Harvey 1864). Phymaspermum acerosum is also used in Zulu culture as a charm to ward off lightning (Hutchings 1996).

Phymaspermum has never been revised and as such was identified as a priority for taxonomic revision in the national strategy for biosystematics research in South Africa (Victor pers. comm.). Several of the species are of conservation concern or data deficient, and preliminary investigations revealed the presence of several new range-restricted species, consistent with the results of various other recent taxonomic studies of southern African Anthemideae genera (Magee and Manning 2010; Magee and Tilney 2012; Powell and Magee 2013; Magoswana and Magee 2014; Magee et al. 2014; Magoswana et al. 2015). Comprehensive taxonomic monographs are vital to species conservation as they directly inform conservation assessments and management as well as policy (Schatz 2002; Mace 2004). Red List assessments completed in the absence of revisions have often been incorrectly categorised, when compared to reassessments done after the taxonomic revision (Kirschner and Kaplan 2002; Powell et al. 2014).

Eumorpha DC. (6 spp.) (Swelankomo 2011), Gymnopentzia Benth. (1 sp.), and Phymaspermum can be distinguished from all other southern African genera by having papillose cypselas with more than 10 primary ribs (Källersjö 1986), and so these characters were used by Oberprieler et al. (2007) to define the subtribe Phymasperminae. Phymaspermum is distinguished by the usual presence of specialized myxogenic, ovoid trichomes on the cypselas. Gymnopentzia is distinguished by longer papillate cypselas and Eumorpha by paleate capitula (only marginal paleae are present in the capitula of Phymaspermum and Gymnopentzia). In addition, the leaves of Phymaspermum are alternately arranged (except in one of the new species described herein) while those of Eumorpha and Gymnopentzia are largely opposite (Källersjö 1986; Swelankomo 2011). As pointed out by Källersjö (1986), three species of Phymaspermum (viz. P. acerosum, P. pinnatifidum, and P. villosum) lack the diagnostic myxogenic ovoid trichomes on the cypselas, leading her to remark that these species may need to be recognised as a separate genus. A cladistic analysis of morphological characters in the subtribe is explored to assess the monophyly of Phymaspermum and possible infrageneric relationships.

A taxonomic revision of Phymaspermum is presented, including comprehensive descriptions, a key to the species, nomenclature, typification, diagnostic characters with illustrations and distribution data.

Materials and Methods

Most of the species were studied in situ and all were studied from selected specimens from B (digital images), NBG, NU, and PRE, as well as the entire collections of BOL, SAM, and WIND (digital images). Maps of each species were produced according to validated information provided on the associated herbarium labels. Collecting localities and associated grid references were checked in literature (Leistner and Morris 1976). These localities were plotted according to the degree reference system as described by Leistner and Morris (1976). The specimens examined are cited under each species treatment and arranged by country, province and then district, and ordered according to geographical position, from west to east and north to south. The quarter degree and associated district are indicated in bold.

Cypselas material was fixed in formalin-acetic acid-alcohol (FAA) for at least 24 hr. Herbarium material was first rehydrated at 60°C for two days before being fixed. Whole cypselas were embedded in glycol methacrylate (GMA) according to a modification (a five day final infiltration) of the method described in Feder and O’Brien (1968). They were then stained using the periodic acid-Schiff/toluidine blue (PAS/TB) method of Feder and O’Brien (1968). All sections were viewed under a
Table 1. Taxon by character matrix used for the morphological and anatomical phylogenetic analyses. See Appendix 1 for a description of characters and character states.

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Leitz wetzlar light microscope and photographed with a JVC KY-F1030 digital camera with AcQuis digital imaging software version 4.0.1.7. Cypselas surface structure was also studied using a scanning electron microscope (SEM). Cypselas were mounted on copper stubs and gold coated using an Emscope gold coater. These were then viewed in a Tescan SEM at 8 kV using the VegaTC software program and photographed with an Oxford instruments X-Max camera.

To construct a phylogeny of Phymaspermum and its relationship to the other two genera within Phymasperminae, Eumorphia and Gymnopentzia, 12 vegetative and reproductive characters for 24 taxa within the tribe were scored (Table 1; Appendix 1) using the outgroup comparison method, with a species of Athanasia (A. elsiae Källersjö) as outgroup (Källersjö 1991). We selected a member from the subtribe Athanasinae to root the trees as ITS sequence data (Oberprieler et al. 2007) and available morphological evidence suggest a close relationship to Phymasperminae, Eumorphia and Gymnopentzia were scored based on literature (Swelankomo 2011, Källersjö 1986). Characters were scored as polymorphic when both states occurred in a single taxon and as unknown (?) if the character was not applicable.

Phylogenetic analyses were conducted using the parsimony algorithm of the software package PAUP* for Windows version 4.0b10 (Swofford 1998) with the PauUp graphical interface (Calendini and Martin 2005). Characters were equally weighted (Wagner parsimony, Farris 1970) and optimized with both accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) with no difference between the two. Tree searches were performed using a heuristic search with 1,000 random sequence additions, tree bisection and reconnection (TBR) branch swapping and 10 trees held per replicate. Internal support was assessed with 1,000 bootstrap (BP) replicates under the same search parameters.

The arrangement of the species of Phymaspermum in the taxonomic revision reflects the presumed phylogenetic relationships as recovered in the morphological strict consensus tree.

Results and Discussion

Morphology and Anatomy—Vegetative Characters—All species of Phymaspermum are evergreen, perennial shrubs or shrublets and fall into two main growth forms: (1) Multi-stemmed shrubs with woody rootstocks and virgate unbranched or poorly branched stems (P. acerosum, P. aciculare, P. argenteum, P. athanasioides, P. comptonii, P. erubescent, P. pinnatifidum, and P. woodii, Fig. 1A–E) or (2) single-stemmed, well branched shrubs or shrublets (P. argenteum, P. appressum, P. leptophyllum, P. oppositifolium, P. parvifolium, P. scoparium, P. thymelaeoides, and P. trifidum, Fig. 1F–N, where the branch apices of P. argenteum (Fig. 1M) and P. scoparium are often spine tipped).

The indument ranges from glabrous to densely hairy, although in P. argenteum, P. comptonii, P. thymelaeoides and P. trifidum (Fig. 1F–H) it is conspicuously densely sericeous. Phymaspermum aciculare, P. erubescent and P. peglerae are readily distinguished from one another by their indumenta, i.e. glabrous in P. aciculare, silvery villous or hispid in P. erubescent and bronze villous in P. peglerae.

With the exception of the new species, P. oppositifolium, all the species of Phymaspermum have sessile, alternate leaves. Most of the species have spreading or erect leaves, except in P. appressum (Fig. 1I, J) and P. oppositifolium where they are characteristically closely appressed. Phymaspermum argenteum is the only species which has characteristically very few and reduced leaves (Fig. 1M, N). The leaves are usually pinnatisect to trifid. Invariably simple entire leaves are diagnostic for P. argenteum, P. appressum, P. oppositifolium, and P. scoparium. In P. leptophyllum and P. thymelaeoides, the leaves are usually simple and entire, rarely lobed. The leaves of P. appressum and P. oppositifolium are characteristically very bony, becoming scarious along the peduncles, while in the rest of the genus they are either fleshy or leathery.

Reproductive Characters—The capitula of Phymaspermum are usually terminal and more or less solitary or aggregated into corymb (Fig. 1A–D). In P. scoparium, however, the capitula are axillary and subsessile. The multistemmed species are all corymbose, except for P. aciculare, P. erubescent, and P. peglerae. In the latter three discoid species and all the radiate species, the capitula are either solitary on the peduncles or with one to three additional capitula borne from leaf axils below (Fig. 1E, H–N). The capitula of P. appressum (Fig. 1I, J) and P. oppositifolium appear to be borne on short axillary fascicles due to their indistinct peduncles.

Most Phymaspermum species have up to four series of involucral bracts, although there can be up to five series in P. athanasioides or six series in P. woodii. The bracts are usually tightly arranged in an imbricate manner and have conspicuous longitudinal resin ducts. In P. acerosum, P. comptonii, and P. pinnatifidum, however, the bracts are irregularly arranged and the number of series are more difficult to distinguish. The involucral bracts of Phymaspermum species are generally rigid with membranous apices and edges, but in P. appressum and P. oppositifolium, the bracts become scarious and brittle. All Phymaspermum species have membranous apices especially on the innermost bracts. The margins of the involucral bracts are prominently dark brown in P. argenteum and sometimes light brown or indistinct in P. woodii and P. leptophyllum. The involucral bracts of P. comptonii have a prominent brown midrib. A brown midrib can also be seen in P. pinnatifidum due to the large bulging resin canal. These bulging resin canals also give the outer bracts a distinctive curved appearance. The involucral bracts can also be hairy or glabrous and have scarious apices and margins. Phymaspermum thymelaeoides has silvery villous involucral bracts which are bronze in P. peglerae. Other species such as P. comptonii, P. scoparium, and P. trifidum have silvery pubescent involucral bracts. The rest of the species generally have glabrous involucral bracts.
As also found in Gymnopentzia, paleae of Phymaspermum species are restricted to the margins and are usually in one series, but sometimes in two series as in P. woodii. However, we have sometimes observed rudimentary paleae in the centre of the receptacles in P. acerosum and P. thymelaeoides. Unlike involucral bracts which usually only have scarious margins and apices, most paleae are scarious and sometimes have ciliate margins (P. acerosum) and apices with reduced longitudinal resin canals. The shape and size of these paleae are variable within species.

The capitula are largely either radiate or discoid, although in one species, P. athanasioides, they are disform. This character is constant for all the species except P. aciculare, where plants can have either discoid or sometimes radiate capitula. When ray florets are present in this species, however, they are very few and reduced in size.

The ray florets are pistillate and fertile, with a white to cream limb which may sometimes have a purplish tinge near the base or underside; in P. appressum and P. oppositifolium they are often entirely purplish. The limbs are usually ovate to obovate and apically three-toothed, although in P. aciculare they are obelliptic.

The disc florets are bisexual and five-lobed. The tube is usually readily distinguishable from the limb and equal in length, although in P. athanasioides and P. woodii, the tube can be longer than the limb, and in P. appressum and P. oppositifolium the distinction between the tube and the limb is not clear. The corollas are always somewhat glandular, but pilose hairs can be found in P. scoparium and P. thymelaeoides. The lobes are triangular and usually spreading, except in P. appressum and P. oppositifolium where they are erect. Similarly erect lobes are sometimes also observed in P. athanasioides. Resin canals in the lobes of the disc florets are absent in all species except in P. acerosum, which rarely has red resin ducts in the tube, limb, and lobes. The anthers of all species have a more or less sagittate base and the appendages were not found to be taxonomically useful.

The cypsela are ellipsoid to obovoid and usually prominently 10–14 ribbed, except in P. leptophyllum where ribs are not prominent (Fig. 2D, L). The fruits are usually 1.6–2.5 mm long and 0.5–0.7 mm wide, although in three species, P. aciculare, P. erubescens (Fig. 2E), and P. pinnatifidum, they are prominently larger, being more than 2.5 mm long (up to 3.5 mm) and 1.0 mm wide. The fruits of P. pinnatifidum can also be up to 3.5 mm long (Fig. 2F) but they are never as wide as those of P. aciculare, P. erubescens, and P. pinnatifidum. A pappus is lacking in all the species, although there may be a thickened apical rim on the cypsela. Phymaspermum pinnatifidum is unique in that it has a conspicuous and extended membranous apical rim (Figs. 2F). The cypsela of Phymaspermum are unique in that they have ovoid, stalked myxogenic trichomes (Fig. 2A–E, 1, L, M), a synapomorphy for the genus. These short stalked myxogenic trichomes are white when dry with an ovoid head consisting of a few cells (Fig. 2I, L, M). Phymaspermum is the only genus within Anthemideae with these stalked trichomes on the cypsela rather than the more usual myxogenic epidermal cells. Only those trichomes on the fruits of the radiate species were observed to rupture (Fig. 2L) when in contact with water. In the discoid species no evidence of rupturing was observed (Fig. 2I, M). These stalked trichomes are particularly dense on the cypsela of the radiate species (Fig. 2B–D). The stalked trichomes are more sparse on the discoid species and can sometimes even be completely lacking in some individuals (Fig. 2E, H, M, N). However, in P. acerosum (Fig. 2G, J, K) and P. pinnatifidum (Fig. 2F) the stalked trichomes have been consistently lost.

In transverse section the epidermal cells are usually more anticlinally elongated in the radiate species of Phymaspermum. In P. leptophyllum (Fig. 2L), these cells are much more distinct and uniform and unlike the other species where they are shorter and distinctly papillate. The cypsela ribs of P. leptophyllum are therefore not as distinct as those in other species. The stalks of the myxogenic trichomes are embedded between these cells and as a result appear sessile. These distinct epidermal cells of P. leptophyllum allow this species to be distinguished from other closely related species such as P. aphylloides and P. thymelaeoides.

The testa epidermis and endocarpic cells remain parenchymatous but in some species they become sclerified. In the mesocarp, the sclerenchyma of Phymaspermum is organised into discrete bundles in which the vascular tissue is found (Fig. 2I–N). The endocarp is seen as a single layer of cells with dark staining contents (Fig. 2I–N).

In three species, resin canals were observed in the cypsela ribs, viz. P. acerosum (Fig. 2J, K), P. comptonii (Fig. 2I), and P. pinnatifidum. The presence of a resin canal in the cypsela of P. comptonii is significant, as it is the only species that combines both resin canals and myxogenic trichomes.

Phylogenetic Relationships—Of the 12 scored characters, 10 were parsimony-informative and two parsimony-uninformative. Two equally parsimonious trees were obtained (differing only in the placement of P. scoparium — either sister to the radiate clade or unresolved) with a tree length (TL) of 17 steps, a consistency index (CI) value of 0.71 and a retention index (RI) value of 0.9. The strict consensus tree is presented in Fig. 3.

Eumorpha and Phymaspermum are recovered to be monophyletic although without bootstrap support and the monotypic Gymnopentzia is not embedded within either Eumorpha or Phymaspermum. Despite the shared presence of opposite leaves, Eumorpha and Gymnopentzia were not recovered as sister genera. Rather, Gymnopentzia was placed sister to Phymaspermum based on the synapomorphic loss of receptacular paleae (character 4). This sister relationship between Gymnopentzia and Phymaspermum was also recognised by Bremer and Humphries (1993) in an alternative equally parsimonious cladogram. Phymaspermum is recovered as monophyletic, supported by the presence of myxogenic trichomes on the cypsela (character 10) (secondarily lost in P. acerosum and P. pinnatifidum). Within Phymaspermum three lineages are identified, although their relationships to one another are unresolved. The first comprises the anomalous P. scoparium, the second a clade of radiate (character 6), single-stemmed species and the third a clade of multistemmed (character 1), largely discoid species (sometimes sparsely radiate in P. aciculare) with sparsely glandular fruits (character 11). Within the discoid clade, P. aciculare, P. erubescens, and P. pinnatifidum form a sister group (BP 67) to the rest of the species based on their larger fruits (character 7) and a subclade comprising P. acerosum – P. woodii is recovered based on the corymbose synflorescence structure (character 3). Within the latter subclade the presence of resin canals in the fruits (character 12) group P. acerosum, P. comptonii, and P. pinnatifidum together. Resolution within the radiate clade is largely unresolved, except for the obvious sister
Fig. 2. Scanning electron micrographs (A–H) and transverse sections (I–N) of selected Phymaspermum cypselas. A. P. scoparium, B. P. appressum, C. P. trifidum. D. P. leptophyllum, note the obscure ribs and apparently sessile trichomes. E. P. erubescens, with the sparse stalked trichomes. F. P. pinnatifidum, showing the absence of stalked trichomes and the prominent apical crown. G. P. acerosum, note the absence of stalked trichomes. H. P. comptonii, showing the absence of stalked trichomes. I. P. comptonii, illustrating the presence of both stalked trichomes between the ribs and the resin canal. J–K. P. acerosum, note the absence of stalked trichomes and the resin canals. L. P. leptophyllum, with anticlinally elongated epidermal cells with trichome stalks inbedded between cells (note also the ruptured trichomes on the bottom left). M. P. erubescens. N. P. peglerae. Vouchers: A. Theron 1055 (PRE); B. Germishuizen 6615 (NBG); C. Magee and Boatwright 512 (NBG); D. Magee and Boatwright 372 (NBG); E. M. Acocks 12161 (PRE); F. Young 1441 (NBG); G. Ward 11272 (PRE); H. Compton 31199 (PRE); I. Burrows 8119 (PRE); J. Dieterlin 822 (PRE); K. Nicholson 2249 (PRE); L. Bohnen 9371 (NBG); N. Pegler 1601 (BOL). Scale: A–H = 500 μm; I–N = 0.1 mm.
relationship between *P. appressum* and *P. oppositifolium* (BP 90), based on the closely appressed leaves (character 2) and scarious bracts (character 5).

**Taxonomic Treatment**


Evergreen, single- to multistemmed, very sparsely to densely leafy, shrubs or shrublets, 0.2–2.0 m high. Stems unbranched to much-branched; branches erect or spreading, rarely spine-tipped, striate, glabrous to densely matted; fascicles usually present in leaf axils, sometimes becoming woolly (in *P. acerosum* and *P. woodii*). Leaves sessile, alternate or rarely opposite (*P. oppositifolium*), very sparsely to closely imbricate, appressed to spreading, 1.0–40.0 × 0.2–3.0 mm, linear to spatulate, entire to pinnatifid, margins involute to revolute, sometimes narrowed into petiole-like base with secondary basal lobes, glabrous to villous, bony, leathery or fleshy; basal swelling continuous with stem ribs present; lobes 0–9, 0.2–24.0 × 0.5–1.5 mm, linear, mucronate to attenuate. Capitula homogamous or heterogamous, radiate, disciform or discoid, terminal or on very short axillary shoots, solitary, with 0–3 additional capitula from leaf axils below or in few- to many-headed (3 to >100), simple or compound corymbs, pedunculate or rarely subsessile; peduncles 1.0–95.0 mm long, glabrous to densely matted. Involucre cylindrical or urceolate to campanulate or hemispherical, sometimes tapering at the base; involucral bracts 3- to 7-seriate, loosely or tightly arranged, 1.0–7.0 mm long, ovate to linear, obtuse to attenuate, margins and apices scarious (bracts entirely scarious in *P. appressum* and *P. oppositifolium*), inner bracts with membranous apices 0.3–2.5 mm long, glabrous to densely villous, green to dark brown, purple, sometimes with brown margins, median resin canals present. Receptacle flat to convex, alveolate, paleate; paleae in marginal series (rarely rudimentary inner paleae present), 2.6–6.3 mm long, linear to obovate, apices obtuse to attenuate, entirely scarious or margins and apices scarious. Ray florets (when present) 3–22, pistillate; tube 1.0–4.2 mm long, sessile glandular trichomes present; limb 3.0–12.0 × 1.8–4.3 mm, ovate to obovate, usually apically 3-dentate, rarely 2-dentate or entire, white to purple. Filiform florets (only in *P. athanasiaoides*) ± 20, pistillate; corolla 2.3–3.0 mm long, yellow, with sessile glandular trichomes, zygomorphic; adaxial lobes 2, abaxial lamina 3-dentate, without resin canals. Disc florets 3 to >100, bisexual, without resin canals (except sometimes in *P. acerosum*); corolla 1.6–4.0 mm long, with sessile glandular trichomes, zygomorphic; glabrous or rarely pilose, yellow to purple; tube 0.7–2.6 mm long; limb 0.5–1.8 mm long (excluding lobes), very narrowly to broadly campanulate, 5-lobed; lobes erect to spreading, 0.3–1.0 mm long, narrowly to broadly triangular or triangular ovate. Anthers 2.0–4.3 mm long (including apical appendage), sagitate at base; apical appendages lanceolate to rounded. Style 1.7–4.0 mm long (excluding the two terminally stigmatic branches), terete with thickened base; branches 0.1–1.9 mm long, truncate, with dorsal papillae. Cypselas 1.6–3.5 ×0.5–1.0 mm,
oblong to broadly obovoid, shortly papillate, apical rim absent or thickened to membranous, conspicuously or inconspicuously (in P. leptophyllum) 10- to 14-ribbed, stalked glandular trichomes present or rarely absent, usually mucilaginous, discontinuous resin canals in ribs rarely present (in P. acerosum, P. comptonii, and P. pinnatifidum).

Diagnostic Characters—Phymaspermum shares the papillose, many ribbed (≥ 10) cypselas with Eumorphia and Gymnopentzia but can be distinguished by the alternate leaves (except in one species, P. oppositifolium) and the presence of unique stalked myxogenic trichomes on the cypselas (subsequently lost in two species, P. acerosum and P. pinnatifidum). It can be further distinguished from Eumorphia by the absence of inner paleae (inner paleae present in Eumorphia) and from Gymnopentzia by the shortly papillose cypselas (long papillose cypselas in Gymnopentzia).

Distribution and Ecology—Phymaspermum is largely restricted to southern Africa, with one species extending into Zimbabwe. Six of the species are endemic to the Greater Cape Floristic region.

KEY TO THE SPECIES OF PHYMASPERMUM

1. Capitula in prominent corymbs ........................................... 2
2. Capitula heterogamous with filiform outer florets; primary leaves mostly entire, some 2- or 3-fid ................. 12. P. athanasioides
3. Capitula homogamous; primary leaves mostly trifid to pinnate ................................................................. 3
4. Leaves ± 0.3 mm wide, densely or sparsely villous; involucral bracts with indistinct to light brown margins; restricted to KwaZulu-Natal and Eastern Cape ................................................. 13. P. woodi
5. Leaf lobes ≥ 1 mm wide, usually silvery sericeous; involucral apically spreading, bracts with prominent dark brown margins; restricted to Limpopo and Mpumalanga ............................................. 14. P. argenteum
6. Involucral bracts strongly unequal, involucral bracts ± equal, innermost with prominent scarious appendages; floret tube without hairs ............................... 3.
7. Stem and leaves glabrous; capitula oblong to narrowly ovate; fruits without stalked trichomes; leaves glabrescent to villous without broad scarious appendages; floret tube usually prominently hairy ................................................... 13
8. Leaves alternate; involucral bracts ovate ........................................... 7. P. appressum
9. Leaves opposite; involucral bracts lanceolate to oblong 8. P. oppositifolium
10. Leaves erect to spreading; involucral bracts hyssopifolius to bony with only narrow scarious margins and apices, with prominent resin canals ........................................... 11.
11. Leaves erect to spreading; involucral bracts bony with only narrow scarious margins and apices, with prominent resin canals ........................................... 13.
12. Capitula cylindrical, bracts ± equal, innermost with prominent rounded scarious appendages; fruits with stalked trichomes ........................................... 17. P. acerosum
13. Capitula cylindrical, bracts ± equal, innermost with prominent rounded scarious appendages; fruits with stalked trichomes ........................................... 15. P. comptonii
14. Leaves silvery pilose or hispid; leaves 2-10 mm long; fruits ≤ 4 mm long .................................................. 10. P. erebescens
15. Leaves silvery villous or hispid; leaves ≥ 8 mm long; fruits ≥ 4 mm long .................................................. 11. P. peglerae
16. Leaves ±1.0–2.0 mm wide; peduncles not becoming spinose, fruits with oblong trichomes apparently sessile 5. P. leptophyllum
17. Leaves ±1.0–2.0 mm wide; peduncles not becoming spinose, fruits with oblong trichomes apparently sessile 6. P. pinnatifidum
18. Leaves ± 0.5 mm wide; peduncles often becoming spinose; fruits with distinct ribs and obviously stalked myxogenic trichomes ............................... 4. P. tridium
19. Leaves ± 0.5 mm wide; peduncles often becoming spinose; fruits with distinct ribs and obviously stalked myxogenic trichomes ............................... 6. P. pinnatifidum

Single-stemmed, sparsely leafy shrublet, height unknown. Stem much-branched; branches erect to spreading, spine-tipped, silvery-pubescent; fascicles sometimes present in leaf axils. Leaves alternate, appressed to spreading, 1.0–5.0 × 1.0–2.0 mm, triangular ovate to spatulate, rounded to mucronate, entire, narrowed into petiole-like base, without secondary basal lobes, densely silvery pubescent on both surfaces, fleshy; basal swelling present, continuous with stem ribs. Capitula discoid, homogamous, on short axillary shoots, solitary, subsessile. involucre 4.0 × 3.0 mm, cyathiform, tapering at the base; involucral bracts 4-seriate, tightly arranged, margins and apices scarious, membranous apices of all bracts 0.1–0.2 mm long, glabrous to villous along edges, brown margins absent, median resin canals present; outer bracts deltoid to lanceolate, ca. 1.5 mm long, acute to obtuse; middle bracts deltoid to lanceolate, ca. 1.8 mm long, acute to obtuse; inner bracts lanceolate to oblong, ca. 1.8 mm long, obtuse; innermost bracts oblong, ca. 2.2 mm long, obtuse. Receptacle convex; paleae in marginal series, linear, ca. 3.0 mm long, obtuse, rigid with scarious margins and apices, scarious apices 0.6 mm long. Disc florets ±10, without resin canals; corolla ±1.8 mm long, with glandular trichomes and hairs on tube and limb, yellow; tube ±1.0 mm long; limb narrowly campanulate, 0.8 mm long (excluding lobes); lobes spreading, 0.7 mm long, triangular-ovate. Anthers 2.1 mm long (including apical appendage); apical appendage oblong. Style 2.2–2.5 mm long (excluding branches); branches 0.8 mm long. Cypselas 2.0 × 0.8 mm, narrowly obovate, 11-ribbed, apical rim thickened, slightly dentate, glandular trichomes present, dense, scattered, not mucilaginous when soaked, discontinuous resin canals in ribs absent. Figure 4.

Diagnostic Characters—Phymaspermum scoparium is unlikely to be confused with any of the other discoid species. It is easily recognised by the subsessile, axillary heads, apically spinescent stems, and florets with a pilose corolla.

Distribution and Ecology—Phymaspermum scoparium is a very poorly collected species from near Graaff-Reinet in the Eastern Cape to Hanover in the Northern Cape (Fig. 4F). The species appears to favor seasonally moist sites. Flowering time is from November to March.

Additional Specimens Examined—SOUTH AFRICA. Northern Cape: 3024 (De Aar: Rhenosterberg (–AC), Drège s.n. (P-image)); between Colesberg and Hanover (–DD), Henrici 3924 (PRE); 3124 (Hanover: Sebeketiriev, Klein Tafelberg, Winterveld (–AD), Ecklon and Zeyher 127 (SAM); Noupoort (–BB), Henrici 4446 (PRE). Eastern Cape: 3125 (Steynsburg: Middelberg (–AC), Acocks 15324 (PRE); Middelburg, Leufontein (–AC), Theron 1055 (PRE). 3224 (Graaff-Reinet: Sneeuwberg (–AA), Drège 45070 (SAM); Sneeuwberg lowlands (–AA), Drège 59179 (PRE), Drège s.n. (–2 two images).


Single-stemmed, densely leafy shrublet, 0.15–0.4 m high. Stem strongly-branched; branches erect to spreading, glabrous to densely silvery pubescent; fascicles sometimes present in leaf axils. Leaves alternate, spreading to rarely reflexed, 3.0–15.0 × 0.8 mm, linear to oblong, mucronate, entire to trifid, sometimes narrowed into petiole-like base, sometimes with secondary basal lobes, glabrous to silvery pubescent on both surfaces, fleshy; basal swelling present, continuous with stem ribs; lobes 2 or 3, 0.2–3.0 × 0.8 mm, oblong, mucronate. Capitula radiate, heterogamous, terminal, solitary, with up to 3 additional capitula from leaf axils below, pedunculate; peduncles 5.0–45.0 mm long, glabrous to silvery pubescent. Involucre 2.5–5.0 × 2.5–6.0 mm, narrowly campanulate (rarely hemispherical), tapering at the base;
involucral bracts 4-seriate, tightly arranged, margins and apices scarious, membranous apices of all bracts 0.3–0.6 mm long, usually with fimbriate margins, glabrous to hairy (rarely beyond margins), brown margins absent, median resin canals present; outer bracts deltoid, 1.0–1.6 mm long, acute to attenuate; middle bracts deltoid, 1.5–1.8 mm long, acute to attenuate; inner bracts oblance, 2.2–2.5 mm long, acute to rounded; innermost bracts oblance, 2.8–3.1 mm long, acute to rounded. Receptacle convex; palea in marginal series, oblong to linear, 2.6–3.0 mm long, rounded, rigid with scarious margins and apices, scarious apices 0.2–0.3 mm long. Ray florets ±7; tube 1.0–1.2 mm long; limb obovate, 4.5–5.3 × 2.3–3.0 mm, apically 3-dentate, white. Disc florets 10–15, without resin canals; corolla 1.6–2.2 mm long, with only glandular trichomes, yellow to purple; tube 1.0–1.2 mm long; limb campanulate, 0.6–1.0 mm long (excluding lobes); lobes spreading, 0.6–0.7 mm long, triangular. Anthers 2.3–2.8 mm long (including apical appendage); apical appendage ovate. Style 1.7–2.3 mm long (excluding branches); branches 0.5–0.6 mm long. Cypselas 2.0 × 1.0 mm, narrowly to broadly obovate, 10–14-rnbed, apical rim thickened, slightly dentate, glandular trichomes present, dense, scattered, mucilaginous when soaked, discontinuous resin canals in ribs absent. Figure 5.

**Diagnostic Characters**—Phymaspermum parvifolium is a compact shrub, less than 0.4 m tall, with a close branching habit and radiate heads. It can sometimes be confused with *P. thymelaeoides* but can be distinguished by its compact growth (*P. thymelaeoides* is an open branched shrub, usually more than 0.8 m tall), the linear to oblance leaves (spathulate in *P. thymelaeoides*), glabrous disc florets (often hairy in *P. thymelaeoides*) and glabrous to sparsely hairy (rarely beyond margins) involucral bracts (densely villous in *P. thymelaeoides*).

**Distribution and Ecology**—Phymaspermum parvifolium is widely distributed in the largely arid areas of the Western Cape, Eastern Cape and Northern Cape as well as the Free State at an altitude of 300–1,500 m (Fig. 5G). Flowering is throughout the year but peaks from March to May. This species is an important fodder plant for sheep and is commonly known as the “swart karoo,” “vaal karoo,” “wit heuning karoo,” and “good karoo” (Smith 1966; Powrie 2004).

**Additional Specimens Examined**—SOUTH AFRICA. Freestate: 2925 (Jagersfontein: Bloemfontein, Hagersdam farm near Hagersdam (–BD), Zietsman 4070 (PRE); Fauresmith (–CB), Mackayth 94 (BOL); Hofman s.n. (PRE), Verdoorn 2093 (PRE); Fauresmith (–CB), Pappendorf 700 (PRE); Fauresmith (–CB), Leistner 1653 (PRE); Fauresmith, farm Bakbank, crest of small hill behind homestead (–DC), Smith 3997 (PRE); Fauresmith, farm Bakbank, small plateau on hill behind farm house (–DC), Smith 4005 (PRE); farm Bakbank, in veld near gate (–DC), Smith 5549 (PRE). 2926 (Bloomfontein): Bloemfontein (–AA), Pole-Evans 1678 (PRE). 3025 (Colesburg): 17 km from Bethulie on road to Philipolis (–BC), Reid 238 (PRE). 12626 (Aliwal North): D. Ray florets. E. Disc floret. F. Cypselas. G. Known geographical distribution. Vouchers: A1, A6, B1, C4. Bester 6152 (NBG); A2–A3, A5, C1, D1, E, F1. Koekemoer 2322 (PRE); A4, A7. Reid 223 (PRE); B2. Compton 2031 (NBG); C2, D2, F2. Vivers y Vlok 410 (PRE); C3. Leistner 1653 (NBG). Scale: A–B = 4 cm; C–D = 1 mm; E = 500 μm.

Hugo 310 (PRE). Western Cape: 3221 (Merweville): Grootfontein, Fraserburg, Layton, Spitskop (–BC), Shearing 74 (PRE); Fraserburg district, Layton, kloof bottom, Spitskop, (–BC), Shearing 161 (PRE). 3222 (Beaufort West): Karoo National Park, NE border of the farm...
3. Phymaspermum thymelaeoides (DC.) Magee & Ruiters comb. nov. Osteospermum thymelaeoides DC., Prodr. 6: 462 (1838).—TYPE: SOUTH AFRICA. Western Cape, Beaufort West (3222): ‘Nieuwveldbergen’ [Nieuwveld mountains] (–AB), Oct 1826, Drège 6177 (holotype: G–DC; image; isotypes: P–image!, two sheets). [Note: de Candolle was uncertain about the placement of this taxon in Osteospermum. Norlindh (1943) in his revision of Osteospermum, recognised that O. thymelaeoides was rather a species of Phymaspermum but incorrectly considered it to be synonymous with Phymaspermum parvisolum. On closer examination the specimen clearly matches P. Schroeteri with the openly branched habit and serious leaves and involucral bracts. As O. thymelaeoides is the older name it has priority and P. Schroeteri is therefore reduced into synonymy. This is the only specimen of this species in de Candolle’s herbarium at G–DC.]


Single-stemmed, densely leafy shrub, (0.5)0.8–1.2 m high. Stem much-branched; branches erect to spreading, silvery pubescent; fascicles sometimes present in leaf axils. Leaves alternate, erect to spreading, 5.0–30.0 × 0.8–3.0 mm, linear to spathulate, mucronate, entire to trifid, narrowed into petiole-like base, sometimes with secondary basal lobes, silvery sericeous on both surfaces, fleshy; basal swelling present, continuous with stem ribs; lobes 3, 2.0–3.0 × 1.0 mm, linear, mucronate. Capitula radiate, heterogamous, terminal, solitary, with 0–2 additional capitula from leaf axils below, pedunculate; peduncles 5.0–35.0 mm long, silvery pubescent. Involucre 4.0–7.0 × 4.0–5.0 mm, hemispherical to cyathiform, sometimes tapering at the base; involucral bracts 3- or 4-seriate, loosely to tightly arranged, margins and apices scarious, membranous apices of all bracts 0.1–1.0 mm long, silvery villous, brown margins absent, median resin canals present; outer bracts lanceolate, 1.5–2.1 mm long, attenuate; middle bracts lanceolate, 2.0–2.3 mm long, rounded; inner bracts oblone, 2.7–3.8 mm long, rounded; innermost bracts oblong, 3.4–4.0 mm long, rounded. Receptacle convex; palaee in marginal series (rarely rudimentary inner palaee present); oblong, 3.5–4.0 mm long, rounded, scarious. Ray florets 8–12; tube 1.2–1.6 mm long; limb obovate, 5.4–7.2 × 2.2–3.0 mm, apically 3-dentate, white to purple. Disc florets 20–30, without resin canals; corolla 1.7–2.7 mm long, with glandular trichomes and sometimes hairs on tube, yellow to purple; tube 0.7–1.8 mm long; limb campanulate, 0.5–1.0 mm long (excluding lobes); lobes spreading, 0.5–1.0 mm long, triangular. Anthers 1.7–3.8 mm long (including apical appendage); apical appendage ovate. Style 1.2–3.2 mm long (excluding branches); branches 0.4–0.5 mm long. Cypselas 2.5 × 0.7 mm, obovate, 11-ribbed, apical rim thickened, slightly denticate, glandular trichomes present, dense, mostly between ribs, mucilaginous when soaked, discontinuous resin canals in ribs absent. Figure 6.

Diagnostic Characters—Phymaspermum thymelaeoides is an openly branched shrub, more than 0.8 m tall, with radiate heads, usually hairy disc floret tubes, and entire, spathulate leaves. It can be distinguished from P. leptophyllum by the spathulate, silvery sericeous leaves and the ribbed cypselas with prominently stalked myxogenic trichomes. Similarly silvery leaves are found in P. trifidum but in P. thymelaeoides the leaves are largely entire and the innermost involucral bracts have a much shorter membranous appendage.

Distribution and Ecology—Phymaspermum thymelaeoides occurs on upper south facing slopes, at altitudes of 1,000–1,700 m, from Ghaapkop near Laingsburg along the Roggeveld and Nuweveld mountains to Molteno Pass (Fig. 6G). Flowering appears to be throughout the year. The species is well grazed (Shearing 1159, PRE; Shearing 1181, PRE; Acoks 17199, PRE) and the flowers have a prominent honey scent.

Additional Specimens Examined—SOUTH AFRICA. Northern Cape: 3221 (Merweville): Oudekloof Bo, Oukloof (–BB), Shearing 941 (PRE); Shearing 1159 (PRE); Fraserburgh, Layton Vergenoeg (–BB), Acoks 25358 (PRE); Layton flats, Vlak Camp (–BB), Acoks 25358 (PRE). Western Cape: 3221 (Merweville): Nuweveld mountains, Uitspannings River Pass, 40 km NW of Merweville (–CA), Brasse 3409 (BOL); Sutherland, Besemgedberg on Komsberg escarpment (–CA), Acoks 17199 (PRE). 3222 (Beaufort West): Nieuwveld mountains (–AB), Esterhuyzen 2746 (BOL); Nieuwveld mountains, next to Molteno Pass, between entrance gates to farms Highlands and Rhenosterdal (–BA), Vlak 2527 (PRE); Theekloof (–BA), Acoks 14151 (PRE). 3320 (Montagu): Boerhoes farm, between Komsbergfontein and Sutherland (–BA), Meine 381 (NBG); Ghaap Kop, Laingsburg (–BA), Compton 14421 (NBG), Schroeter 18591 (BOL); Ghaap Kop, Laingsburg, Whitehill (–BA), Compton 4427 (BOL, NBG), Esterhuyzen 3270 (BOL).
4. Phymaspermum trifidum Magee and Ruiters sp. nov.—

**TYPE:** SOUTH AFRICA. Western Cape, Worcester (3319): Farm Goedemoed, between Robertson and McGregor (–DD), 28 November 2012, Magee and Boatwright 512 (holotype: NBG!; isotypes: BOL!, K!, PRE!, S!)

Single-stemmed, densely leafy shrub, 0.7 m high. Stem much-branched; branches erect to spreading, silvery pubescent; fascicles sometimes present in leaf axis. Leaves alternate, spreading, 5.0–17.0 × 0.8–1.0 mm, linear, mucronate, rarely entire (entire on peduncles), trifid, narrowed into petiole-like base, without secondary basal lobes, silvery sericeous on both surfaces, fleshy; basal swelling present, continuous with stem ribs; lobes 3, 1.0–8.0 × 0.8–1.0 mm, linear, mucronate. Capitula radiate, heterogamous, terminal, solitary, pedunculate; peduncles 20.0–40.0 mm long, silvery pubescent. Involucre 5.0–6.0 × 6.0–7.0 mm, hemispherical to cyathiform, not tapering at the base; involucral bracts 3- or 4-seriate, tightly arranged, margins and apices scarious, membranous apices of all bracts 0.3–1.3 mm long, pubescent, brown margins present, median resin canals present; outer bracts lanceolate to ovate, 2.1–2.4 mm long, acute to rounded; middle bracts lanceolate to ovate, 2.2–2.6 mm long, rounded; inner bracts ovate, 3.0–4.0 mm long, rounded; innermost bracts linear to oblong, 4.5–4.8 mm long, rounded. Receptacle convex; paleae in marginal series, linear to oblong, 4.3–5.9 mm long, rounded, rigid with scarious mar-
appears to be from August to November. This species is reported to be well grazed (Van Breda 4130, PRE).

Additional Specimens Examined—SOUTH AFRICA. Western Cape: 3319 (Worcester): Farm Goedemoed, between Robertson and McGregor (–DD), Helme 7480 (NBG). 3320 (Montagu): Bonnievale, Kapteinsdrif (–CC), Van Breda 4130 (PRE); Robertson, along road to Stormsvlei (–CC), Van Breda 805 (PRE two sheets).


Phymaspermum junceum sensu Less. (1832) non Osteospermum junceum Berg. [See Magee et al. 2013]

Single-stemmed, leafy shrub, 0.5–1.6 m high. Stem much-branched; branches erect to spreading, silvery pubescent; fascicles sometimes present in leaf axils. Leaves alternate, spreading to erect, 6.0–25.0 × 1.1–2.0 mm, linear, mucronate, revolute, entire to trifid, without petiole-like base, sometimes with secondary basal lobes, silver hairs on both surfaces, fleshy to leathery; basal swelling present, continuous with stem ribs; lobes 2–3, 2.0–7.0 × 1.0 mm, linear, mucronate. Capitula radiate, heterogamous, terminal, solitary, with 0–3 additional capitula from leaf axils below, pedunculate; peduncles 15–95 mm long, silvery pubescent. Involucre 5.0–6.0 × 6.0–9.0 mm, hemispherical, rarely tapering at the base; involucral bracts 4-seriate, tightly arranged, margins and apices scarious, membranous apices of all bracts 0.5–1.8 mm long, villous silvery hairs, brown margins sometimes present, median resin canals present; outer bracts triangular to lanceolate, 3.3–3.4 mm long, acute; middle bracts lanceolate to oblanceolate, 4.3–4.5 mm long, acute; inner bracts oblanceolate, 5.7–6.2 mm long, acute to obtuse; innermost bracts oblanceolate, 6.5–7.0 mm long, rounded. Receptacle convex; paleae in marginal series, narrowly oblanceolate, 5.2–6.0 mm long, rounded, scarious. Ray florets 10–22, tube 1.1–4.2 mm long; limb obovate, 10.0–12.0 × 3.0–4.3 mm, apically 3-dentate, rarely entire or 2-dentate, white to mauve. Disc florets up to 100, without resin canals; corolla 3.5–4.0 mm long, with only glandular trichomes, yellow; tube 1.6–1.7 mm long; limb campanulate, 1.7 mm long (excluding lobes); lobes spreading, 0.7–0.8 mm long, triangular. Anthers 4.3–6.5 mm long (including apical appendage); apical appendage ovate. Style 2.8–3.6 mm long (excluding branches); branches 1.0–1.3 mm long. Cypselas 2.5 × 0.8 mm, oblong to obovate, 10-ribbed, apical rim absent, inconspicuous glandular trichomes present, dense, appearing sessile on ribs, mucilaginous when soaked, discontinuous resin canals in ribs absent. Figure 8.

**Diagnostic Characters—**Phymaspermum leptophyllum is unique in that the epidermal cells of the cypselas are anticlinally elongated so that they obscure the ribs and hide much of the stalk on the trichomes, making them appear sessile. It can be confused with the sympatric and closely related *P. aphyllum* both of which have linear leaves and
lanceolate to oblong involucral bracts (outer bracts of *P. leptophyllum* are sometimes triangular). However, in addition to the anticlinally elongated epidermal cells of the cypselas *P. leptophyllum* differs from *P. aphyllum* in that it is more densely leafy, with persistent leaves, ± 1.0–2.0 mm wide, the branches are not longitudinally white striped and the peduncles do not become spinescent (Fig. 1L).

**Distribution and Ecology**—*Phymaspermum leptophyllum* is endemic to the Little Karoo where it occurs on quartz outcrops (Vlok and Schutte-Vlok 2010), at an altitude of 400–650 m, from Montagu to Oudtshoorn (Fig. 8G). Flowering is from May to November.

**Additional Specimens Examined**—SOUTH AFRICA. Western Cape: 3320 (Montagu): Wildheendenkloof Pass, 44 km E of Montagu (–AD); Nordenstam and Lundgren 1194 (Ladismith); 3321 (Ladismith): Ladismith (–AD); Bayliss 2814 (NBG); Levy 7488 (BOL); Levy 7487 a (BOL); Ladismith, koppie behind the town (–AD), Levy 11145 (BOL). Little Karoo, Nooukloof Nature Reserve, level spur N of road, 2.8 km from north gate where road reaches its highest point (–CA), Laidler 465 (PRE); Klein Karoo, Kliphoopte by Springfontein (–DC), Ecklon 622 (MO–image, P–image, S–image).

**6. Phymaspermum aphyllum** Magee and Ruiters sp. nov.—

**TYPE**: SOUTH AFRICA. Western Cape, Montagu (3320): Along road between Ladismith and Laingsburg, in road reserve (–BD), 2 June 2007, Vlok & Schutte 596 (holotype: NBG; isotype: K!)

Single-stemmed, very sparsely leafy shrub, 0.5–1.0 m high. Stem much-branched; branches erect to spreading, spine-tipped, densely white wooly between ribs; fascicles rarely present in leaf axils. Leaves alternate, very sparse, caducous, apressed to erect, 2.0–20.0 × 0.5 mm, linear, mucronate, revolute, entire, without petiole-like base, without secondary basal lobes, glabrous on both surfaces, fleshy to leathery; basal swelling present, continuous with stem ribs. Capitula radicate, heterogamous, terminal, solitary, with 0–1 additional capitula from leaf axils below, pedunculate; peduncules 25.0–38.0 mm long, silvery pubescent. Involucre 5.0–6.0 × 6.0–9.0 mm, hemispherical, rarely tapering at the base; involucral bracts 4-seriate, tightly arranged, margins and apices scarious, membranous apices of all bracts 0.3–0.5 mm long, silvery villous, brown margins absent, median resin canals present; outer bracts lanceolate, 1.5–1.6 mm long, acute; middle bracts lanceolate, 2.0–2.2 mm long, acute; inner bracts lanceolate to oblong, 2.5–3.5 mm long, acute to obtuse; innermost bracts oblong, 3.5 mm long, rounded. Receptacle convex; paleae in marginal series, narrowly oblong, 3.0–4.5 mm long, rounded, scarious. Ray florets 9–10; tube 2.0–2.8 mm long; limb obovate, 5.7–11.4 × 3.2–4.0 mm, apically 3-dentate, white. Disc florets ± 50, without resin canals; corolla 1.6–2.0 mm long, with only glandular trichomes, yellow; tube 0.7–1.0 mm long; limb campanulate, 0.7–1.8 mm long (excluding lobes); lobes spreading, 0.5–0.7 mm long, triangular. Anthers 2.0–2.4 mm long (including apical appendage); apical appendage oblong. Style 2.0–2.2 mm long (excluding branches); branches 0.4 mm long. Cypselas 2.0–2.5 × 0.5–0.8 mm, obovate, 10–11-ribbed, apical rim absent, glandular trichomes present, dense, scattered, mucilaginous when soaked, discontinuous resin canals in ribs absent. Figure 9.

**Diagnostic Characters**—*Phymaspermum aphyllum* has in the past been incorrectly identified as *Phymaspermum aphyllum* (Berg.) Less. (the latter now a synonym of *Osteospermum junceum*, Magee et al. 2013). It is a sparsely leafy shrub with caducous leaves, ± 0.5 mm wide, longitudinally white striped stems which are densely white wooly between the ribs and persistent peduncles which often become spinescent. It differs further from the closely related *P. leptophyllum* by the obviously ribbed cypsela with prominently stalked myxogenic trichomes. In *P. leptophyllum* the cypsela appear unribbed and the myxogenic trichomes appear sessile due to the prominently elongated epidermal cells.

**Distribution and Ecology**—*Phymaspermum aphyllum* is known from only a handful of localities between Barrydale and the Witteberg in the Little Karoo at an altitude of around 700 m (Fig. 9G). The leaves of this species are apparently highly palatable for livestock (Vlok and Schutte-Vlok pers. comm.). Flowering is from June to December.

**Additional Specimens Examined**—SOUTH AFRICA. Western Cape: 3320 (Montagu): 14 miles SSE of Laingsburg (–BD), Aocks 20509 (PRE); Ladismith, Farm Comae, near Plathuis Station (–DB), Van Breda 4407 (PRE); Swellendam, “Poortfontein”, along Barrydale/ Ladismith road (–DD), Van Breda 4545 (PRE).

Single-stemmed, densely leafy shrublet, 0.3–1.2 m high. Stem much-branched; branches erect to spreading, glabrous to silvery tomentose; fascicles present in leaf axils. Leaves alternate, closely imbricate, appressed, 1.0–3.0 × 0.5–2.0 mm, ovate to lanceolate, acute to mucronate, entire, without petiole-like base, without secondary basal lobes, glabrous on both surfaces, bony; basal swelling present, continuous with stem ribs. Capitula radiate, heteromarginal, terminal on short axillary shoots, solitary, with 0–3 additional capitula from leaf axils below, prominent peduncles absent. Involucre 4.0–7.0 × 4.0–8.0 mm, hemispherical to cyathiform, tapering at the base; involucral bracts 3-seriate, tightly arranged, margins and apices scarious, membranous apices of all bracts 0.7–1.0 mm long, scarious texture, brown margins absent, median resin canals present; outer bracts broadly ovate sometimes oblong, 2.5–3.0 mm long, rounded; middle bracts broadly obovate sometimes oblong, 3.0–3.5 mm long, rounded; inner bracts narrowly obovate sometimes oblong, 4.3–4.5 mm long, rounded. Receptacle convex to flat; palaee in marginal series, 3.8–4.0 mm long, rounded, scarious. Ray florets 11–14; tube 1.7–2.0 mm long; limb ovate to obovate, 7.0–8.5 × 2.7–3.0 mm, apically 3-dentate, rarely entire sometimes with longer middle tooth, white to purpure. Disc florets 22–47, without resin canals; corolla 2.0–2.3 mm long, with only glandular trichomes, yellow to purpure; tube 0.9–1.0 mm long; limb very narrowly campanulate, 1.0–1.2 mm long (excluding lobes); lobes erect, 0.3–0.5 mm long, triangular. Anthers 2.4–4.3 mm long (including apical appendage); apical appendage ovate. Style 2.2–3.8 mm long (excluding branches); branches 0.4–1.9 mm long. Cypselas 2.0 × 0.5 mm, narrowly obovate, 12-ribbed, apical rim thickened, slightly dentate, brown, glandular trichomes present, dense, mostly between ribs, mucilaginous when soaked, discontinuous resin canals in ribs absent. Figure 10.

**Diagnostic Characters**—*Phymaspermum appressum* is easily recognised by the prominently appressed leaves, entirely scarious involucral bracts and purplish ray florets. It can only be confused with the closely related *P. oppositifolium*, from which it differs in the alternate leaves, the hemispherical to cyathiform involucres, and the ovate to obovate involucral bracts.

**Distribution and Ecology**—*Phymaspermum appressum* is endemic to sandstone slopes and ridges above 940 m within the Little Karoo, from Anysberg to the Witteberg (Fig. 10G). Flowering is from April to December.

**Additional Specimens Examined**—SOUTH AFRICA. Western Cape: 3320 (Montague): Laingsburg, Wittepoort (–BB), Compton 11834 (BOL, NBG); Anysberg Nature Reserve, at start of Prince’s Poort (–BC), Germishuizen 6615 (PRE); south slopes of Anysberg, Ladismith (–BC), Wurts 1411 (NBG); Buffels Poort Bay, Ladismith (–BD), Levyns 7429 (BOL). 3321 (Ladismith): Townerkop State Forest, at Besemfontein, near hut (–AD), Hockstra 76 (PRE); Klein Swartberg above Besemfontein, mountains just E of Seweweekspoort (–AC), Oliver 9698 (NBG); south slope of Elandsberg range, N of Klein Swartberg (–AD), Wurts 1529 (NBG); Gamka Mountain Reserve, Zebra ridge, eastern sector (–DB), Cattell and Cattell 99 (PRE). 3322 (Oudtshoorn): Swartberg Pass (–AC), Bolus 1052 (M-image), Levyns 5037 (BOL), Tyson 12796 (SAM), Zietsman and Zietsman 1689 (PRE), Esterhuysen 4515 (BOL), Prince Albert (–AC), Storlau 57099 (SAM two sheets); Prince Albert, Swartberg Pass, north side (–AC), Acocks 15529 (PRE), Jackson 14 (BOL), Bond 1540 (PRE); near summit, Goldblatt and Porter 12477 (NBG); Hiking trail from Malvdraai, Goldblatt and Porter 11851 (NBG); Swartberg Pass, Teegb lookout point (–AC), Magee and Battwig 369 (NBG); Top of Boshuise pass, Prince Albert (–AC), Levyns 11160 (BOL); east slopes of Platberg (–AC), Storlton 10321 (NBG).

8. **Phymaspermum oppositifolium** Magee and Ruitters sp. nov. —**TYPE:** SOUTH AFRICA. Eastern Cape, Steytlerville (3324): Kouga Mountain, Riverside (–CD), 20 January 2000, Eusten-Brown 02 (holotype: NBG!)

Single-stemmed, densely leafy shrub, 1.5 m high. Stem much-branched; branches erect to spreading, glabrous; fascicles present in leaf axils. Leaves opposite, closely imbricate, appressed to sometimes erect, 2.0–5.0 × 1.0–2.0 mm, lanceolate, acute to acuminate, sometimes mucronate, entire, without petiole-like base, without secondary basal lobes, glabrous on both surfaces, bony; basal swelling present, discontinuous resin canals in ribs present. Vouchers: A. Magee and Ruitters 2000 (M-image), Levyns 5037 (BOL), Tyson 12796 (SAM), Zietsman and Zietsman 1689 (PRE), Esterhuysen 4515 (BOL); Prince Albert (–AC), Storlau 57099 (SAM two sheets); Prince Albert, Swartberg Pass, north side (–AC), Acocks 15529 (BOL), Bond 1540 (PRE); near summit, Goldblatt and Porter 12477 (NBG); Hiking trail from Malvdraai, Goldblatt and Porter 11851 (NBG); Swartberg Pass, Teegb lookout point (–AC), Magee and Battwig 369 (NBG); Top of Boshuise pass, Prince Albert (–AC), Levyns 11160 (BOL); east slopes of Platberg (–AC), Storlton 10321 (NBG).
continuous with stem ribs. Capitula radiate, heterogamous, terminal on short axillary shoots, solitary, with 0–3 additional capitula from leaf axils below, prominent peduncles absent. Involucres 5.0–6.0 × 4.0–5.0 mm, funnel-shaped, tapering at the base; involucral bracts 4-seriate, tightly arranged, margins and apices scarios, membranous apices of all bracts 2.4–2.5 mm long, scarios texture, brown margins absent, median resin canals present; outer bracts lanceolate, 3.4 mm long, acute; middle bracts lanceolate, 4.0–4.5 mm long, acute; inner bracts lanceolate, 5.5 mm long, rounded. Receptacle convex; paleae in marginal series, linear, ± 4.0 mm long, rounded, scarios. Ray florets ± 8; tube 1.5 mm long; limb ovate to obovate, 4.8 ± 2.3 mm, apically 3-dentate, white to purple. Disc florets ± 20, 3.4 mm long, acute; middle bracts lanceolate, 4.0 mm long, acutely; outer bracts lanceolate, 5.5 mm long, rounded. Receptacle convex; paleae in marginal series, linear, ± 4.0 mm long, rounded, scarios. Ray florets ± 8; tube 1.5 mm long; limb ovate to obovate, 4.8 × 2.3 mm, apically 3-dentate, white to purple. Disc florets ± 20, 3.4 mm long, acute; middle bracts lanceolate, 4.0 mm long, acutely; outer bracts lanceolate, 5.5 mm long, rounded.

**Distribution and Ecology**—This species is known only from the type collection in the Kouga mountains of the Eastern Cape (Fig. 11G), where it was collected at an altitude of 250 m. It was found flowering in January and the collector noticed seeing very few plants (Eusten-Brown pers. comm.).

**Diagnostic Characters**—Phymaspermum oppositifolium is the only opposite leaved species within the genus. It shares the appressed leaves, entirely scarios involucral bracts and purplish ray florets with the closely related *P. appressum* from which it can be distinguished further by the funnel-shaped involucres and lanceolate involucral bracts.

**Fig. 11.** Phymaspermum oppositifolium. A. Leaf. B. Capitula. C. Involucral bracts (outermost to innermost series, from left) and single palea (far right). D. Disc floret. E. Ray floret. F. Cypsela. G. Known geographical distribution. Voucher: A–F. Eusten-Brown 02 (NBG). Scale: A–B = 4 mm; C–D = 1 mm; E = 500 μm.
trichomes present, sparse, scattered, not mucilaginous when soaked, discontinuous resin canals in ribs absent. Figure 12.

**Diagnostic Characters** — *Phymaspermum aciculare* is the only species in the genus which can have either discoid or radiate heads. It can be distinguished from the other radiate species by the sparsely radiate heads with no more than four rays, with limbs less than 5 mm long. Amongst the discoid species it shares the non-corymbose capitula and large cypsela (>0.8 mm wide) with *P. erubescens* and *P. plegerea*. It can however be readily distinguished by the glabrous stem and leaves and the smaller (3.0–6.0 mm wide), obconical, sometimes few radiate capitula with 3–5 additional capitula from leaf axils below.

**Distribution and Ecology** — *Phymaspermum aciculare* is widely distributed from McGregor in the Western Cape to Bloemhof in the North West Province with a disjunction in Namibia (Fig. 12G). A similar Namibian disjunction has also been reported in *Melolobium* (Moteete and Van Wyk 2006) as well as *Dichilus* (Schutte and Van Wyk 1988). This species prefers hard, dry soil and sometimes occurs on dolerite, at altitudes of 40 m to 1,700 m.

Flowering is from September to May.

**Additional Specimens Examined** — NAMIBIA. 2217 (Windhoek): Dobra river bank (–AC), Koene 580 (WIND); Farm Hohenau (–CB), Walter and Walter 1177 (B–image, PRE); Lichtenstein (–CC), Dinter 3527 (B–two images, PRE, SAM).

SOUTH AFRICA. North West: 2725 (Bloemhof): Leeuwfontein, 10 km W from Wolmaranstad (–BB), Van Wyk 1431 (FEE); Free State: 2824 (Kimberley): McGregor Hills, Kamfersdam (–DB), Esterhuysen 3683 (BOL); 2826 (Brandfort): Krugersdrift dam Nature Reserve on Deelkop (–CC), Muller 1507 (PRE); 2925 (Jagersfontein): Bloemfontein, Bestersput near Petrusberg (–BA), Acocks 8475 (BOL, PRE); Fauresmith (–CB), Henrici 4710 (PRE); Fauresmith, Rotorua (–CC), Henrici 2844 (BOL). Northern Cape: 2822 (Glen Lyon): Hay division, Floradale (–BD), Esterhuysen 2359 (BOL two sheets); 2823 (Griekwastad): Past Sharon farm on road to Postmasburg at high powerline (–AB), Germishuizen 8586 (PRE); 2824 (Kimberley): Rust en Vrede (–DA), Anon. H1251 (PRE); 2924 (Hopetown): Kraanvogel Valley (–CD), Acocks 1681 (BOL); 3022 (Carnarvon): Grootsfontein S of Prieska, Leeuput (–BQ), Roux 36 (PRE); 3123 (Victoria West): 36 km from Victoria West on main road to Britstown, farm Rietpoort (–AA), Herman 1152 (PRE); 3228 (Sutherland): Salpeterkop SE slope, between Amandelboom and De Hoek, Fraserburg (–BD), Moffet and Stemsona 3964 (PRE). Western Cape: 3222 (Beaufort West): Nieuwveld (–AB), Marloth 4753 (PRE, BOL); Drège 389 (SAM); north end of Molteno Pass (–BA), Acocks 14338 (PRE); Bleak house farm (–BA), Russel, Robinson and Herman 337 (PRE); Sunnyside (–BC), Esterhuysen 2718 (BOL). Eastern Cape: 3026 (Alivai North): Bushmanskop (–CD), Dalvies 4207 (BOL); Nieouveaarspruit, between Orange and Caledon rivers (–DB), Zylher s.n. (HBG–image), Ecklon and Zylher s.n. (HAL–image); Eland’s Hoek (–DC), Bolus 235 (BOL). 3225 (Mahlobyanini East): Cradock, Mountain Zebra Park, on plains below house of Berghof (–AD), Liebenberg 7673 (B–image, PRE); Cradock, Bergkwagga Park (–AD), Liebenberg 7144 (FEE); 5 of Cradock (–BA), MacGill 685 (NBG); Cradock (–BA), Zylher 225 (SAM two sheets), Zylher 961 (K–image, S–image); near Mortimer in Cradock (–BC), Kollitz 9292 (BOL). 3124 (Hanover): Herbert, Eureka (–CB), Acocks 8749 (BOL); Sneeuwbergen (–DC), Bolus 1846 (NBG); north slopes of Sneeuwberg, Leopards valley (–DC), Bolus 3431 (BOL). 3125 (Steynburg): 4 miles from Middleburg on Rietpoort road (–AC), Commiss 763 (BOL); Grootsfontein, Middelburg (–AC), Tieron 331 (PRE). 3226 (Fort Beaufort): Leliswane (–CA), Tyson 38747 (SAM). 3325 (Fort Elizabeth): Uitenhage, Ecklon 1142 (G–DC).

PRECISE LOCALITY UNKNOWN: Luagawalakle, MacOwan 1087 (PRE); MacOwan 38749 (SAM).


Multistemmed, leafy shrublet, up to 0.3 m high. Stems few-branched; branches erect, sparsely hairy to silver villous or
hispid; fascicles sometimes present in leaf axils. Leaves alternate, apressed to erect, 2.0–10.0 × 1.0 mm, linear to lanceolate, acute to acuminate; revolute, entire, without petiole-like base, without secondary basal lobes, glabrous to silver-villosum adaxially, glabrous abaxially, fleshy to leathery; basal swelling present, continuous with stem ribs. Capitula discoid, homogamous, terminal, solitary, with 0–3 additional capitula from leaf axils below, pedunculate; peduncles 15.0–60.0 mm long, glabrous. Involucre 5.0–7.0 × 5.0–7.0 mm, hemispherical to cyathiform, rarely tapering at the base; involucral bracts 4-seriate, tightly arranged, margins and apices scarious, membranous apices of all bracts 0.8–1.3 mm long, glabrous, brown margins absent, median resin canals present; outer bracts deltoid to lanceolate, 2.7–3.5 mm long, acute to attenuating; middle bracts triangular ovate, 4.0–4.3 mm long, acuminate; inner bracts lanceolate, 4.6–5.2 mm long, rounded. Receptacle convex; palea in marginal series, oblongolate to oblong, 4.6–5.2 mm long, rounded, membranous with scarious margins and apices, scarious apices 0.6–1.2 mm long. Disc florets ±20, without resin canals; corolla 2.0–3.0 mm long, with only glandular trichomes, yellow; tube 1.0–1.2 mm long; limb narrowly campanulate, 1.0–1.2 mm long (excluding lobes); lobes spreading, 0.6–1.0 mm long, triangular ovate. Anthers 2.8–3.6 mm long (including apical appendage); apical appendage obovate. Style 2.4–2.8 mm long (excluding branches); branches 0.4–1.0 mm long. Cypselas 3.6 × 1.0 mm, obovate, 11-ribbed, apical rim thickened, dentate, glandular trichomes present, sparse, scattered, not mucilaginous when soaked, discontinuous resin canals in ribs absent. Figure 13.

**Diagnostic Characters**—*Phymaspermum erubescens* could be confused with *P. pegleri* or discoid specimens of *P. aciculare* but can be readily distinguished by the sparse to dense silvery villous or hispid indumentum on the stems and leaves (densely bronze villous in *P. pegleri* and glabrous in *P. aciculare*), the shorter leaves, 2.0–10.0 mm long and smaller cypselas (when compared to *P. pegleri*) ≤4 mm long.

**Distribution and Ecology**—*Phymaspermum erubescens* is a relatively poorly collected species which occurs from Lady Frere to King Williams Town in the Eastern Cape (Fig. 13F). It favours sandstone in grasslands at altitudes of 600–1,700 m. Flowering is from October to March.

**Additional Specimens Examined**—SOUTH AFRICA. Eastern Cape: 3127 (Lady Frere: Farm Ebuheni ca. 27 km N of Indwe along R 396, track up to Vodacom tower (~AD), Magee et al. 436 (NBG); Farm Ebuheni, SW mountain slopes, N of homestead (~AD), Bester 7396 (PRE); hills near Cala (~DA), Esterhuysen 29184 (BOL); Ngcobo (~DB), Acocks 12161 (PRE). 3227 (Stutterheim): King Williams Town (~CD), Flanagan 2164 (NBG).

**Precise Locality Unknown**—Kaffraria, Sim 19851 (PRE).


Multistemmed, densely leafy shrublet, 0.6–0.7 m high. Stems few-branched; branches erect, silvery villous; fascicles sometimes present in leaf axils. Leaves alternate, erect,
not mucilaginous when soaked, discontinuous resin canals in ribs absent. Figure 14.

**Diagnostic Characters**—*Phymaspermum peglerae* shares the disoid non-corymbose heads and large fruit with *P. erubescens* and *P. aciculare* but can be distinguished by the densely bronze villous indumentum (sparse to dense silvery villous or hispid indumentum in *P. erubescens* and glabrous in *P. aciculare*), the usually larger leaves 9.0–18.0 mm long and the largest fruit in the genus >4 mm.

**Distribution and Ecology**—*Phymaspermum peglerae* is known from only two very old collections along the banks of the Mthatha River in the Eastern Cape (Fig. 14F). This species flowers in midsummer, around January.


Multistemmed, densely leafy shrub, 0.2–2.0 m high. Stems much-branched; branches erect, grey-pubescent; fascicles never present in leaf axils. Leaves alternate, spreading, 6.0–40.0 × 0.8–2.0 mm, linear to oblong, acute to mucronate, entire to trifid, involute, narrowed into petiole-like base, without secondary basal lobes, glabrous on both surfaces, leathery; basal swelling present, continuous with stem ribs; lobes 2–3, 0.5–1.0 × 0.5–1.0 mm, linear to oblong, acute to mucronate. Capitula disciform, heterogamous, terminal, many-headed ± 30, simple to compound corymb, pedunculate; peduncles 4.0–35.0 mm long, glabrous to white tomentose. Involucre 4.0–8.0 × 3.5–8.0 mm, hemispherical, cyathiform to urceolate, sometimes tapering at the base; involucral bracts 4–6-seriate, with the peduncular bracts usually being the first two series, tightly arranged, margins and apices scarious, membranous apices of all bracts 0.3–1.2 mm long, glabrous to tomentose especially along the edges, brown margins absent, median resin canals present; outer bracts lanceolate, 2.0–3.0 mm long, acute; middle bracts deltoid to lanceolate, 2.2–4.2 mm long, acute; inner bracts deltoid to lanceolate, 2.2–4.3 mm long, acute to rounded; second inner bracts deltoid to lanceolate, 3.8–4.6 mm long, acuminate to rounded. Receptacle convex; paxae in marginal series, oblong to linear, 3.2–3.7 mm long, acute to attenuating, scarious. Filiform florets ± 20; corolla 2.3–3.0 mm long, with glandular trichomes, zygomorphic; adaxial lobes 2, 0.7–1.0 mm long, triangular, spreading, abaxial lamina 0.3–0.6 mm long, linear, 3-dentate. Disc florets ±100, without resin canals; corolla 2.2–3.0 mm long, with only glandular trichomes, yellow; tube 1.0–2.0 mm long; limb narrowly campanulate, 0.8–1.3 mm long (excluding lobes); lobes erect to spreading,
0.4–0.6 mm long, triangular. Anthers ± 3.0 mm long (including apical appendage); apical appendage rounded to oblong. Scale: A–B = 4 mm; C–D = 1 mm; E = 500 μm.

**Diagnostic Characters**—Phymaspermum athanasioides was previously considered to be a part of a complex with *P. bolusii* and *P. montanum*, distinguished by apparent differences in their involucral bracts. However, upon further study, these characters were found to be highly variable and no clearly recognisable characters could be found to distinguish between them. As a result only a single variable species, *P. athanasioides*, is recognised here. It is readily distinguished from all other species in the genus by the marginal filiform florets and from the other species with corymbosely arranged capitula by the absence of fascicles in the leaf axis and by the mostly entire leaves, which rarely become 2- or 3-fid.

**Distribution and Ecology**—Phymaspermum athanasioides is widely distributed from around Harrismith in KwaZulu Natal to Musina in Limpopo and extending into Swaziland and further north into Zimbabwe (Fig. 15G). It grows in mixed bushveld and grassland, especially on quartzite or sandstone, at an altitude of 1,000 m to 1,750 m. Flowering is throughout the year but especially in August, hence its vernacular name August Gold.

**Additional Specimens Examined**—SOUTH AFRICA. Limpopo: 2230 (Musina): Souptansberg, Entabeni Forest Reserve (~CC), Codd 3058 (PRE); Venda, Musekwa location (~CC), Du Toit 298 (PRE); Hangklip, Louis–Kriel, Waterberg Transvaal (~CC), Maguire 1426 (NBG), 2329 (Polokwane): Souptansberg Mountain, Letsame at foot of cliffs (~AB), Venter 6233 (PRE), Rogers 19904 (PRE); Vivo, Farm Llwellyn 35 on Souptansberg (~AB), Venter 10,755 (PRE); Makhado (~BB), Breger 23464 (PRE); Blaauwberg, south slopes at plateau (~CD), Esthershausen 21,435 (BOL), Tomazon farm (~DD), Niënaber 26 (PRE); Haenertsburg, Iron Crown Mountain (~DD), Venter 10,855 (PRE), 2330 (Tzaneen: Polokwane, Wolkberg (~CC), Van der Merwe 33 (PRE), 3249 (Zebiedela): Mokopanet district, summit of highest peak, Zebediela mountains (~AA), Galpin s.n. (BOL); 40 km NE of Mokopane, Snymanstrand (~AA), Maguire 2997 (B–image). 2430 (Pilgrims Rest): Shuluvane (~AB), Jonus 13887 (PRE); Lekgamaaets Fluid Reserve (~AB), Stalmans 83 (PRE); Lekgamaaets Nature Reserve, Balloon/mountain 1493 m, shrubland on cliff face (~AB), Stalmans 1340 (PRE). North West: 2526 (Zeenzuth): On road between Koster and Lichtenburg, Mabaalstat (~DC), Vreemheer 1438 (PRE); 13 miles from Koster on Mabaalstat road (~DC), Story 5642 (PRE); Gauteng: 2527 (Rustenburg): Rustenburg (~BA), Collins 23957 (PRE), Galpin s.n. (BOL); Magaliesberg nature area (~DC), Ortiz and Anderson 534 (PRE), 2528 (City of Tshwane): Magaliesberg, Vissenhoek, upper slopes on top of range (~CA), Repton 1292 (PRE), 2627 (Potelshistroom): Witpoortjie Falls, Roodekrantz 83, Krugerdorp, 20 miles NNE of Johannesburg, Orange Grove (~BB), Mogg 21,326 (PRE); 3 km N of Krugerdorp (~BB), Codd 3149 (PRE); Paardeburg 20 miles from Johannesburg (~BD), Tuifosis 1017 (NBG). 2628 (Johannesburg): Johannesburg west koppies (~AA), Laub 3977 (SAM); Elsburg (~AA), Rogers 12143 (BOL); Jeppewood reserve (~AA), Gillillain 6026 (K–image); Johannesburg (~AA), Mass 12006 (PRE); Witwatersrand, Hospital Hill, Orange Grove (~AA), Bryant Co. (BOL), Mass 5072 (BOL), Cowraith 405 (K–image); Kensington (~AA), Oster 6427 (PRE); Melville Koppies central, along path 100 metres from lapa near Kafue Road entrance (~AA), Magee 394 (NBG); Heidelberg (~AC), Schlechter 3517 (BOL). Mpumalanga: 2430 (Pilgrims Rest): Lulunature, farm Grootvlygenboom (~CA), Moss 5072 (NBG); 216934 (BOL); The Downs, near Tzaneen (~DA), Rogers 20101 (BOL), Nd 103 (NBG); Mount Sheba estate (~DC), Boucher 1836 (NBG), Kerfoot 8755 (PRE); Morganzen Reserve (~DC), Mohle 407 (PRE); Motlatovierpoort Nature Reserve, Mulhisky (~DB), Zietsman 3771 (PRE), 2530 (Mashishing): Between Lydenberg and Sabie, 12 miles from Lydenberg, Long Tom Pass (~AB), Balshiyus and Kersberg 2111 (PRE), Wilkinson 280 (PRE); Mashishing, upper Middelvlei trail, Buffelskloof Nature Reserve (~BC), Breyer 8518 (PRE); Buffelskloof Nature Reserve, on plateau overlooking a gorge, along edge (~BC), Koekemoer 2091 (PRE); Pilgrims Rest (~BC), Rogers 14171 (PRE), Woodbush (~CC), Jenkins 13960 (PRE); Next to Berlin off ramp on Kaapsehoop (~DB), Mothogane NB0019 (PRE); Kaapse Hoop escarpment (~DB), Nd 43 (NBG), Rogers 19504 (PRE), 23141 (BOL); Near Cyrinia Letty Nature Reserve (~DD), Glen 1329 (PRE), 2531 (Komatipoort): Moederlief 109 JU 450m S of Mpangeni beacon (~CA), Delia 3883 (PRE); Louw’s Creek Timbers 3 km N of offices (~CB), Khule 2439 (PRE); SE of Louw’s Creek. S.A.T.I.C.O forestry station, Bearded Man Peak (~CB), McMurtry 12837 (PRE); Three Sisters, SE of Kaapmuiden (~CB),

Pentzia tysonii Thell. in Vierteljahrsschr. Naturf. Ges. Zürich. 61: 454 (1916).—TYPE: SOUTH AFRICA. KwaZulu Natal, Kokstad (3029): Mount Currie (–AD), Mar. 1883, Tyson 1254 (lectotype: Z–image!, designated here; isotypes: BOL! SAM!) [Note: The specimen in Z is selected as it forms part of the collection which Thellung would have studied.]

[Pentzia pinnatifida var. chenoleoides Hutch. p.p. excl. type.]

Multistemmed, densely leafy shrublet, 0.4–0.6 m high. Stems few-branched; branches erect, white to silvery tomentose; fascicles present in leaf axils. Leaves alternate, spreading, 4.0–35.0 × 0.5–0.8 mm, linear, sometimes involute, deeply pinnatifid, narrowed into petiole-like base, sometimes with secondary basal lobes, white to silvery villous on both surfaces, leathery; basal swelling present, continuous with stem ribs; lobes 3–5, 2.0–28.0 × 0.5–1.0 mm, linear, mucronate. Capitula discoid, homogamous, terminal, few- to many-headed (3–40), simple to compound corymbs, pedunculate; peduncles 2.0–33.0 mm long, white to silvery tomentose. Inflorescence 5.0–8.0 × 3.0–5.0 mm, narrowly campanulate to urceolate, apically constricted, sometimes tapering at the base; involucral bracts 4- or 5-seriate, tightly arranged, margins and apices scarious, membranous apices of all bracts 0.3–0.8 mm long, glabrous to slightly or densely pubescent or villous, especially edges, very rigid, brown margins light and inconspicuous, median resin canals present; outer bracts deltoid to lanceolate, 2.2–3.3 mm long, acute to acuminate; middle bracts deltoid to ovate, 2.7–3.4 mm long, acuminate; inner bracts deltoid to lanceolate, 2.7–4.0 mm long, acuminate to rounded; second inner bracts ovate, 3.0–5.0 mm long, rounded; innermost bracts ovate, 4.3–5.8 mm long, rounded. Receptacle convex to flat; paleae in two marginal series, linear to oblong, 4.3–6.0 mm long, rounded, rigid with scarious margins and apices, scarious apices 0.8–1.1 mm long. Disc florets 37–55, without resin canals; corolla 2.3–3.2 mm long, with only glandular trichomes, yellow; tube 1.4–1.8 mm long; limb narrowly campanulate, 1.0–1.4 mm long (excluding lobes); lobes spreading, 0.6–1.0 mm long, narrowly triangular. Anthers 2.7–3.8 mm long (including apical appendage); apical appendage oblong. Style 2.0–3.3 mm long (excluding branches); branches 0.5 mm long.

 Disc florets 37–55, without resin canals; corolla 2.3–3.2 mm long, with only glandular trichomes, yellow; tube 1.4–1.8 mm long; limb narrowly campanulate, 1.0–1.4 mm long (excluding lobes); lobes spreading, 0.6–1.0 mm long, narrowly triangular. Anthers 2.7–3.8 mm long (including apical appendage); apical appendage oblong. Style 2.0–3.3 mm long (excluding branches); branches 0.5 mm long.

Cypselas 1.8–2.0 × 0.5 mm, oblong to obovate, 11-ribbed, apical rim thickened, entire to slightly dentate, glandular trichomes present, sparse, scattered, not mucilaginous when soaked, discontinuous resin canals in ribs absent. Figure 16.

**Diagnostic Characters**—Phymaspermum woodii shares the narrowly campanulate to urceolate involucres and flat, deltoid to ovate, closely appressed involucral bracts with *P. argenteum*...
but can be distinguished by the sparsely villous leaves with narrower lobes (≤0.5 mm wide) and the 5-seriate, apically constricted involucres with at most indistinct brown margins. This species could also be confused with the spring flowering *P. pinnatifidum* with which it shares the smaller habit and narrowly lobed leaves but can be readily distinguished by the much narrower campanulate to urceolate, apically constricted involucres with closely appressed involucral bracts, the absence of a prominent membranous crown on the fruit and the later flowering time (late summer into autumn).

**Distribution and Ecology**—*Phymaspermum woodii* is distributed on rocky hillsides in moist grasslands along the southern and eastern Drakensberg in KwaZulu Natal and Free State (Fig. 16F), at altitudes of 1,700–2,750 m. Flowering is in late summer to autumn from February to May.

**Additional Specimens Examined**—SOUTH AFRICA. Free State: 2828 (Bethlehem): Royal Natal National Park, Tugela gorge (−DB), Hilliard 2851 (NU), KwaZulu Natal: 2829 (Harrismith): Cathedral Peak (−CC), Unknown s.n. (NU); Cathedral Peak Reserve, Mikos Pass (−CC), Magee et al. 460 (NBG); Cathedral Peak Forest Reserve station, on spur leading to Organ Pipes Pass (−CC), Killick 1705 (BOL, PRE). 2929 (Underburg): Giants Castle, contour walk (−AD), Retief 1667 (PRE); Giants Castle Game Reserve, Bamberg area (−AD), Trauseld 758 (PRE); Highmoor Forest Reserve (−BC), Hilliard 4814 (NU); Merinodale (−BC), Wright 483 (NU); Garden Castle Forest Reserve, Mlabonja Valley (−CA), Hilliard and Burtt 15061 (NU); 5–7 miles NNW of Castle View farm, headwaters of Mahlangubu River (−CB), Hilliard and Burtt 15271 (NU–image). 2930 (Pietermaritzburg): Near Currys Post (−AC), Wood 4457 (BOL), Wood 1007 (CRA–image, SAM); Table Mountain (−DA), Acocks 1505 (PRE); 3029 (Kokstad): Summit of Ntsheni Mountain in Ntsikeni Nature Reserve (−AB), Magee et al. 547 (NBG); Summit of Mount Currie (−AD), Magee et al. 447 (NBG).


Multistemmed, densely leafy shrub, 0.3–1.5 m high. Stems few-branched; branches erect, sparsely to densely silvery tomentose; fascicles present in leaf axils. Leaves alternate, spreading, 8.0–18.0 × 0.8–2.0 mm, linear when undissected, mucronate, sometimes revolute, entire to pinnatifid, narrowed into petiole-like base, without secondary basal lobes, sparsely to densely silvery villous on both surfaces, fleshy; basal swellings into petiole-like base, without secondary basal lobes, sparsely mucronate, sometimes revolute, entire to pinnatifid, narrowed to densely silvery-tomentose. Involucre 5.0–6.0 mm long, narrowly to densely silver villous on both surfaces, fleshy; basal swellings into petiole-like base, without secondary basal lobes, sparsely mucronate, sometimes revolute, entire to pinnatifid, narrowed to densely silvery-tomentose. Involucre 5.0–7.0 × 1.8–3.5 mm, narrowly campanulate to cylindrical, tapering at the base; involucral bracts 3– or 4-seriate, tightly arranged, margins and apices scarious, membranous apices of all bracts 0.5–1.0 mm long, glabrous to villous (rarely beyond margins), brown margins dark and distinct, median resin canals present; outer bracts deltoid to lanceolate, 1.7–1.9 mm long, acuminate; middle bracts deltoid to ovate, 2.4–3.1 mm long, acuminate; inner bracts broadly oblong to lanceolate, 2.8–3.8 mm long, acuminate to rounded. Receptacle convex; pales in marginal series, oblong, linear, 3.8–4.5 mm long, rounded, rigid with scarious apices, scarious apices ± 0.5 mm long. Disc florets 6–23, without resin canals; corolla 2.3–3.1 mm long, with only glandular trichomes, yellow; tube 1.2–1.7 mm long; limb narrowly to broadly campanulate, 1.0–1.4 mm long (excluding lobes); lobes spreading, 0.7–1.0 mm long, narrowly to broadly triangular. Anthers 2.8–3.4 mm long (including apical appendage); apical appendage oblong to lanceolate. Style 2.0–3.0 mm long (excluding branches); branches 0.2–0.3 mm long. Cypselas 2.0–2.8 × 0.7 mm, oblong, 10-ribbed, apical rim thickened, entire, brown, glandular trichomes present, sparse, scattered, not mucilaginous when soaked, discontinuous resin canals in ribs absent. Figure 17.

**Diagnostic Characters**—*Phymaspermum argenteum* shares the fleshy, usually silvery sericeous leaves with the closely related *P. comptonii*, but can be readily distinguished by the narrowly campanulate involucres with closely appressed, deltoid to ovate involucral bracts with prominent dark margins.

**Distribution and Ecology**—*Phymaspermum argenteum* occurs from around Polokwane and Zebediela in Limpopo to near Pilgrims Rest in Mpumalanga (Fig. 17F). It is found in grassland vegetation in dolomite soils at an altitude of 1,450–2,080 m. They flow from May to September.

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**Fig. 17.** *Phymaspermum argenteum*. A. Leaves. B. Capitula. C. Involucral bracts (outmost to innermost series, from left) and single pales (far right). D. Disc floret. E. Cypselas. F. Known geographical distribution. Vouchers: A. Brusse 5567 (NBG); B. Burrows and Manning 9004 (NBG); C–E. Brusse 5611 (NBG). Scale: A–B = 4 mm; C–D = 1 mm; E = 500 μm.
Additional Specimens Examined—SOUTH AFRICA. Limpopo: 2329 (Polokwane): Iron Crown (–DD), Mathews 896 (PRE). 2429 (Zebediela): Mokopane, Makapansgat, “nek” at top of rock gully (–AA), Maguire 2913 (B-image), near top of Diabase gully, Maguire 8200 (B-image); Ga-Maja, Donkerkloof road off the main Polokwane- Burgersfort road, near Chuniespoort, 1.5 km from the radio masts to Chuniespoort, Farm Stylkop 344KS (–BA), Brasse 5783 (B-image, NBG); Bewaarkloof, 3 km from the main Boyne-Wolkberg road to Ashmole Dales, at the Ashmole Dales sign (–BB), Brasse 5611 (B-image, BOL, NBG, NU, WIND); Wolkberg plateau 14 km SE of Boyne (–BB), Van Vuuren 1533 (K-image, PRE). Mpumalanga: 2430 (Pilgrims Rest) Mouthatsepoort Dam Reserve, rocky plateau, Mouthatsepoort View Point (–DB), 5524 (PRE); Road from Pilgrims’s rest to Bourke’s Luck, near TGME Sports Club (–DB), Barrows and Manning 9004 (NBG, PRE); 31 km from Ohrigstad on road to Pilgrims Rest (–DC), Clark 1239 (PRE); Lisbon Falls, Graskop (–DD), Compton 19801 (NBG); Lisbon, “Moltrat’s”, on rocky slopes on top of escarpment (–DD), Liebenberg 3555 (PRE).


Multistemmed, densely leafy shrublet, 0.75–1.0 m high. Stems few-branched; branches erect to spreading, sparsely to densely silvery tomentose villous, sometimes with purplish brown margins (Fig. 18A–D). Anthers ± 3.1 mm long, triangular. Disc florets ± 2.0 mm long (excluding branches); D. Disc floret. E. Cypsela. F. Known geographical distribution. Vouchers: A, E. Compton 31199 (PRE); B. Brasse 6335 (PRE); C, D. Compton 32016 (PRE). Scale: A–B = 4 mm; C–D = 1 mm; E = 500 μm.

Distribution and Ecology—Phymaspermum comptonii is a near endemic of Swaziland, extending slightly over the South African border around Barberton (Fig. 18F). It grows in grassland at an altitude of 1,100–1,700 m. Flowering is from December to May.

Additional Specimens Examined—SOUTH AFRICA. Mpumalanga: 2531 (Komatipoort): Barberton Mountailands Nature Reserve (–CC), Barrows 8119 (PRE); Ida Dayer Nature Reserve 38 km SE of Barberton (–CC), Muller 2057 (PRE).

SWAZILAND. 2631 (Mbabane): Mbabane Forbes Reef, Ngwenya mountains near Oshoek border with South Africa, Bomvu Ridge old iron ore mine on path to Bushmen cave, on SW slope as one exits excavated part (–AA); Brasse 6335 (PRE); Bomvu Ridge (–AA); Compton 31199 (PRE), Compton 28823 (PRE two sheets).

[Note: As Hooker’s Icones Plantarum was based on collections from Kew herbarium, sheet K000410760 from that collection is designated here as it also contains the original collection labels (giving both the month and date of collection) and is clearly the material upon which the illustration was based.]

Multistemmed, densely leafy shrub, 0.25–0.5 m high. Stems unbranched; branches erect, glabrous or with few silver-villous hairs, sometimes woolly or matted; fascicles present in leaf axils. Leaves alternate, erect to spreading, 5.0–32.0 × 0.2–1.0 mm, linear, deeply pinnatifid, narrowed into petiole-like base, sometimes with secondary basal lobes, silvery-pubescent villous hairs on both surface, leathery; basal swelling present, continuous with stem ribs; lobes 7–9, 4.0–25.0 mm, filiform to linear, attenuating. Capitula discoid, homogamous, terminal, few- to many-headed (5–30), simple to compound corymb, pedunculate; peduncles 4.0–35.0 mm long, glabrous to matted. Involucre 6–7 × 4–5 mm, funnel-shaped to cylindric, rarely tapering at the base; involucral bracts 3- or 4-seriate, loosely arranged, margins and apices scarious (curved shape due to thin rigid centres with resin canals), membranous apices of all bracts 0.2–2.5 mm long, glabrous to villous especially on edges, brown margins absent, median resin canals present; outer bracts triangular to lanceolate or oblong, 2.3–3.0 mm long, attenuating to rounded; middle bracts lanceolate to oblong, 2.7–3.8 mm long, attenuating to rounded; inner bracts linear to oblong, 4.3–5.0 mm long, acute rounded; innermost bracts oblong, 5.2 mm long, rounded. Receptacle convex; paleae in marginal series, linear to oblong, 3.3–5.1 mm long, rounded, rigid with scarious margins and apices, scarious apices 0.7–1.0 mm long. Disc florets 38–44, without resin canals; corolla 2.3–2.5 mm long, with only glandular trichomes, yellow; tube 1.2–1.5 mm long; limb campanulate, 1.0 mm long (excluding lobes); lobes spreading, 0.6–1.0 mm long, triangular to triangular-ovate. Anthers 2.8–3.2 mm long (including apical appendage); apical appendage lanceolate. Style 2.1–2.6 mm long (excluding branches); branches 0.5–0.7 mm long. Cypselas 3.5 × 0.7 mm, oblong to obovate, 12-ribbed, apical rim membranous, dentate, glandular trichomes absent, discontinuous resin canals in ribs present.

Figure 19.

Diagnostic Characters—Phymaspermum pinnatifidum is a small, spring flowering multistemmed shrublet with discoid corymbose arranged capitula and cypselas with a prominent membranous apical crown. Together with P. acerosum it does not have myxogenic trichomes on the cypselas (the generic synapomorphy) but rather prominent resin canals in the cypselas ribs. It can be readily distinguished from P. acerosum by its earlier flowering time, smaller stature (less than 0.5 m tall) with thin herbaceous stems, the broader funnel or cup-shaped involucres and the prominent membranous apical crown on the cypselas. Its small size means that it could also be confused with P. woodii but can be readily distinguished by the broader, not apically constricted involucres with loosely appressed involucral bracts, the prominent membranous apical crown on the cypselas and the absence of myxogenic trichomes.

Distribution and Ecology—Phymaspermum pinnatifidum is restricted to the Pietermaritzburg district of the KwaZulu Natal Province (Fig. 19F) on the Natal group sandstone and is mostly found in grasslands between 450–920 m. The species is early flowering, usually in spring, between August and October, but early fires can result in even earlier flowering (Hilliard 1977).

Additional Specimens Examined—SOUTH AFRICA. KwaZulu Natal: 2930 (Pietermaritzburg): Mapumulo, Great Noodseberg (–BD), Strey 6048 (PRE); Ndwedwe, Orxwatin (–BD), Strey 7745 (NU); Noodseberg, Orxwatin plateau (–BD), Williams 572 (PRE); Camperdown, Drummond (–DA), Rump s.n. (NU), Gelpin 10297 (PRE); New Hanover, Botha’s Hill (–DA), Young 2235 (PRE), Wood 1480 (SAM); Table Mountain (–DA), Hilliard 3986 (NU), Killick 188 (NU), Killick 673 (NU, PRE); Cato Ridge, Mkabelo near Ekuthuleni (–DA), Williams 393 (PRE); 8 km S of Wartburg, near Ekathuli, on farm Windy Hill (–DA), Balzawill and Balzawill 4655 (B-image); Inanda (–DB), Wood 168 (SAM, BOL), Wood 606 (BM-image); Inanda, Elephant’s Trunk (–DB), Strey 6996 (NU); Ndwedwe, Inanda mountain (–DB), Hilliard 2047 (NU); Richmond, Mid-Illovo centre, Farm...


PRECISE LOCALITY UNKNOWN: Notnads Hill Station, Medley Wood 39121 (SAM).


Pentzia pinnatifida var. chenooleoides Hutch. in Kew Bull. 10: 241 (1916).—TYPE: SOUTH AFRICA. Limpopo, Tzaneen Natal (2330): Near Murchison (–DC), 1884/5, Wood 3110 (lectotype: K–image!, designated in Hilliard and Burtt (1973); isolecotype: NH–image!).


Multistemmed, densely leafy shrub, 0.3–1.8 m high. Stems unbranched to few-branched; branches erect, glabrous or scabrous to silvery villous; fascicles present in leaf axils. Leaves alternate, spreading, 6.0–40.0 × 0.5–1.0 mm, linear when undissected, mucronate, sometimes involute, entire (usually on upper branches) to deeply pinnatifid, narrowed into petiolo-like base when dissected, sometimes with secondary basal lobes, glabrous to silvery villous on both surfaces, leathery; basal swelling present, continuous with stem ribs; lobes 3–9, 2.0–24.0 × 0.5–1.0 mm, linear, mucronate. Capitula discoid, homogamous, terminal, few- to many-headed (5 to +100), simple or compound corymbs, pedunculate; peduncles 8.0–42.0 mm long, tomentose. Involve 1.3–6.0 × 1.5–3.0 mm, narrowly campanulate to cylindrical, tapering at the base; involucral bracts 3–4-seriate, loosely to tightly arranged, margins and apices scarious, membranous apices of inner bracts ± 0.5 mm long, glabrous to villous, brown margins absent, median resin canals present; outer bracts lanceolate, 1.4–2.5 mm long, acute to acuminate; middle bracts lanceolate, 2.4–3.5 mm long, acute to acuminate; inner bracts lanceolate to oblong, 3.3–4.2 mm long, rounded. Receptacle convex; paleae in marginal series (rarely rudimentary inner paleae present), oblong to linear, 4.0–4.8 mm long, acute, rigid with thick scarious margins and apices, scarious apices ± 0.6 mm long. Disc florets 3–18, sometimes with resin canals in the tube, limb and lobes; corolla 2.3–2.6 mm long, with only glandular trichomes, yellow; tube 1.0–1.5 mm long; limb campanulate, 0.8–1.2 mm long (excluding lobes); lobes spreading, 0.6–0.7 mm long, triangular. Anthers 2.5–2.8 mm long (including apical appendage); apical appendage oblong. Style 2.0–2.8 mm long (excluding branches); branches 0.5–0.6 mm long. Cypselas ca. 2.0 × 0.5 mm, oblong, 13– to 14–ribbed, apical rim thickened, entire to slightly dentate, light to dark brown, glandular trichomes absent, discontinuous resin canals in ribs present. Figure 20.

Diagnostic Characters—Phymaspermum acerosum shares the narrowly lobed pinnatifid leaves, the absence of myxogenic trichomes on the cypselas and the presence of prominent resin canals in the cypselas ribs with P. pinnatifidum. It can be distinguished by its narrowly campanulate to oblong involucres and the absence of a prominent apical crown on the cypselas (only at most a thickened apical rim which can be entire to shortly dentate). Phymaspermum acerosum is also a much larger more robust shrub growing to more than 0.5 m tall with much thicker and woodier stems than the smaller P. pinnatifidum which tends to have much more slender and herbaceous stems.

The previously recognised species P. villosum was at first distinguished from P. acerosum by having much broader oblong and hairy involucres. Phymaspermum acerosum was considered to only have narrowly campanulate involucres however, after many specimens were examined, P. acerosum is now considered to have involucres which vary from narrowly campanulate to broad and oblong and P. villosum is now a synonym of P. acerosum.

Distribution and Ecology—Phymaspermum acerosum is widely distributed from Port Elizabeth in the Eastern Cape Province to Noodsberg in the Limpopo Province (Fig. 20 F) where it occurs in grassland and forest margins at an altitude

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of 60–2,200 m. It flowers throughout the year, with a peak between April and July.

Additional Specimens Examined—SOUTH AFRICA. Gauteng: 2528 (City of Tshwane): Doornpoort (~CB), Mogi 2161 (PRE, NBG); Mpmalanga: 2430 (Pilgrims Rest) Ohrigstad Nature Reserve (~DC), Theron 3633 (PRE), Theron 3607 (PRE), Jacobsen 2903 (PRE); Morgenzoon Nature Reserve, near Graskop (~DC), Reid 3 (PRE); Mount Sheba Nature Reserve (~DC), Kerfoot 8757 (PRE); near Graskop (~DD), Phillips 3491 (PRE); Graskop, above Kowpyre Pass, along road (~DD), Koekemoer 2123 (PRE), near Mac-Mac Falls (~DD), Burtt Davy 438 (PRE, BOL), 2530 (Masishanging): 8 miles from Pilgrims Rest on Mashishing road (~AB), Story 1215 (PRE), Masishanging (~AB), Burtt Davy 1165 (BOL), Wilms 791 (BM-image, NU), Masishanging, near turn off to Mount Anderson from Long Tom Pass (~BA), Koekemoer 2280 (PRE); Pilgrims Rest, between Mashishing and Sabie (~BA), Schuff 5465 (PRE); Between Mashishing and Sabie (~BA), Pole Evans 2995 (PRE), Hartebeesvlakte (~BA), Mohle 20 (PRE), Sabie valley (~BB), Galpin 39 (BOL), Rosebaugh (~BB), Rodgers 20377 (PRE), Sim 546 (BOL), Entokozweni (~CB), Young 1476 (PRE), Emakhazi near Entokozweni (~CA), Cold 7759 (PRE), Helopmith, Kaapse Hoop road, 12 miles out (~DB), Liebenberg 2553 (PRE), 2531 (Komatipoort: Barberton (~CC), Williams 10512 (PRE); 7 miles NW of Havelock Mine, Barberton (~CC), Cold 7846 (PRE), 2730 (Vryheid): Hoedjie, Farm Suikerhoek, Wakkerstroom (~AB), Devenish 1698 (NU), Free State: 2828 (Bethlehem): Qwa Qwa National Park Avondrust II (~BC), Zietsman 3349 (PRE), 2829 (Harrismith): Harrismith Botanic Garden (~AC), Zege s.s. (NBG); Renburskog, 7 km van Swinburne (~AC), Jacobs 429 (PRE), 2830 (Pietermaritzburg): Stockville Valley, Farm Stockville 1382 (~AC), Hafström and Acocks 1855 (~AC), Devenish 1133 (~DC), Devenish 401 (~BA), Utrecht, near road to Wakkerstroom to Paulpietersburg, Mooifontein farm, Gaugua, south hills of Pongola mountain series (~AC), Jordan 1825 (~PRE), Nauwouwoort, Utrecht (~AD), Devenish 1133 (~DC, BOL), Koekemoer 2037 (~DC), near farm district, Gaugua farm, 25 km from Wakkerstroom on the Paulpolokwane road (~AD), Meyer 218 (~PRE); south side of Dumbe Mountain (~BD), Acocks 11542 (~PRE), Vryheid, 12 miles from Natal Spa on Vryheid-PaulPolokwane road (~DB), Ross 1251 (~NU), Bloemhof, Ermynathyi (~DD), Thode 2962 (~NU), Leeuwnek Pass, Ermynathyi Mountain (~DD), Shirley (~NU two sheets), 2731 (Lousbursg): 2 miles from Vryheid on road to Lousbursg on north facing slope (~CA), Hardy 37 (~PRE), 19 miles from Vryheid on Lousbursg road, Ngkonghlwana River (~CA), Ross 1224 (~NU), Nkotse, Itala Nature Reserve (~CB), Hilliard and Burtt 10018 (~NU), Hilliard and Burtt 8546 (~NU), Lousbursg (~CB), Compton 19702 (~NU), Nkotse district, Ngome (~CD), Hilliard and Burtt 9849 (~NU), Nkotse, 7 miles W of Ngome (~CD), Codd 9580 (~PRE two sheets), Nkotse, about 10 km from main office of forestry on road to Vryheid (~CD), Gernsd auten 2103 (~PRE), 2829 (Harrismith): Inkupe Hill in the Biggarsberg (~BB), Acocks 10645 (~PRE), Cathedral Peak Reserve, Miles Pass (~CC), Mager et al. 460 (NBG), 2830 (Dundee): Helpmekaaier/Endskraal road (~AD), Hilliard 1575 (~NU), Shirley s.s.n. (~NU); Nqutu (~BA), Codd 1363 (~PRE); hill on east side of Zangeni Peak (~BD), P.H. Acocks 11553 (~NU), Pomery district Jobskop on summit plateau (~CA), Venter 1775 (~PRE), Pangolo mountains to Kaffir drift (~CA), Thode A327 (~PRE); 12 miles Muden/Weenen road (~CA), Moll 3244 (~PRE two sheets, NU), Umhlumla mountain top (~CA), Acocks 13864 (~PRE), Rudeni-Nqutu road (~DB), Edwards 2249 (~NU), 2831 (Nkandla): Mahlabatini, Ceza forest (~AB), Hilliard and Burtt 3312 (~NU); Lower part of Nkandla Forest, 147 miles from Nkandla (~CA, BOL), Winter 2831 (~PRE), 2832 (Mubatuba): Hlabisa, Hluhluwe Game Reserve (~AA), Ward 2620 (~PRE, NU), 2929 (Underberg): 17 km E of Mooi river on Hlatikulu road, Farm Lanner Veane (~BA), Balkwill and Manning 468 (~NU), Central Drakensberg, Highmoor forestry station (~BC), Breitenbach 5072 (~PRE), Estcourt district side of Kambberg Nature Reserve, Rosette road (~BC), Wright 176 (~NU); Impendle district, Loteni area (~BC), Roberts s.s.n. (~NU), 2930 (Pietermaritzburg): Karkloof (~AC), Rhead 7471 (~image), Tl. 1139 (BOL); below Bride Road view site, Karkloof Nature Reserve (~AC), Styles 25 (~NU), Hgonoani Veld near Michaelhouse (~AC), Pents and Acocks 10313 (~PRE); Mount Park Dargle, Lions River (~AC), Johnson 433 (BOL); Lions River, The Dayle (~AC), Hilliard 2157 (~NU), Lions River, Karkloof, near turnoff to farm Gutaine (~AC), Hilliard 4852 (~NU); 15 miles from Currys Post/~Nottingham road, Lions River (~AC), Moll 886 (~NU); 25 km NNE Howick, Twin Falls (~AC), Grove 51 (~NU), Lions River, Curly's Post, Mehyels Bush (~AC), Hilliard 4853 (~NU), Lions River, E of Karkloof Gorge (~AC), Parry 18 (~NU), Whitecliffe, Greytown (~BA), Wood 889 (SAM); De Rust, Greytown (~BA), Thode 2835 (~NU), Greytown (~BA), Wylie 34605 (~PRE), Wylie 21927 (~PRE), 'Mowhay' Ahrens (~BB), Fisher 463 (~NU), Lions River, Silvordale (~BB), Wright 1502 (~NU), Swartkops Hill (~CB), Esterhuysen 20,294 (BOL); Writers Kloof (~CB), Carnegie 1216 (~BOL), Chase Valley (~CB), Castlam 28 (~NU); World's View (~BB), Moll 2647 (~NU); along roadside above Sweet Waters, on the way to Hilton (~CB), Warren 5 (~NU), Town Bush (~BB), Randles 29 (~NU), Byrne, Keerom (~AC), Strey 11269 (~NU), Richardson, Byrne Valley (~AC), Schafold s.s.n. (~NU), Galpin s.s.n. (BOL); Richmond (~CD), Medley Wood 9844 (~NU two sheets); Richmond, Enon Estate (~CD), Hilliard 2037 (~NU), Drummmond (~DA), Bronhead s.s.n. (NU), Camperdown, Drummmond (~DA), Camden Smith 32 (~NU), Table Mountain (~DA), Killick 628 (~NU), Johnstone 195 (~NU), Ndwevedo, Inanda (~DB), Wood 921 (BOL), Hilliard 2052 (~NU); Inanda (~DB), Wood s.s.n. (Z), United (~DB); Near Summit Assagay, Ethekwini Municipality (~DC), Wragg 671 (~NU), Hammarsdale area, HECTOR (ESKOM) substation site (~DC), Ward 1307 (~NU); Camperdown, Nagle Dam (~DC), Wells 1543 (~NU), M. Stainbanks farm, Mid Illovo (~DC), Young 1087 (~NU), Summerveld part of Assagay (~DC), Wragg 88 (~NU), Krantzkoof (~DD), Schlechter 3182 (~BOL), Clarkson 29 (~NU), Galpin s.s.n. (NBG), Galpin 12078 (~BOL), 2530 (Pietermaritzburg): Hoskote (~AD), Hilliard 1501 (~NU), Hilliard 4865 (~NU-3); Gillitis area, Stockville Valley, Farm Stockville 1382 (~DD), Ward 11272 (~NU, PRE), Pinetown, Mbilo River Valley, below Paradise Valley Nature Reserve.
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LITERATURE CITED


Appendix 1. Morphological characters and character states used in the cladistic analysis. 1, Habit: single-stemmed = 0; multistemmed = 1. 2, Leaves: erect to spreading = 0; appressed = 1. 3, Capitula: peduncles undivided to lax corymb = 0; arranged in dense corymb = 1. 4, Capitula paleae: present = 0; only marginal = 1. 5, Involucral bracts: rigid = 0; scarious = 1. 6, Ray florets: absent = 0; present = 1. 7, Cypselas: width ≤ 0.8 mm = 0; width > 0.8 mm = 1. 8, Cypselar ribs: < 10 = 0; > 10 = 1. 9, Cypselar surface: not papillose = 0; papillose = 1. 10, Glandular trichomes: absent = 0; present = 1. 11, Glandular trichomes distribution: dense = 0; sparse = 1. 12, Resin canals in ribs: present = 0; absent = 1.