

A revision of Fumariaceae (Fumarioideae) in southern Africa, including naturalized taxa

J.C.MANNING*, P. GOLDBLATT** and F. FOREST***

Keywords: *Cysticapnos* Mill., *Discocapnos* Cham. & Schltld., *Fumaria* L., Fumariaceae, southern Africa, taxonomy, *Trigonocapnos* Schltr.

ABSTRACT

The native and naturalized species of Fumariaceae in southern Africa are reviewed, and keys and full descriptions are provided. All relevant regional synonyms are given and the indigenous species are illustrated. Three native genera with four species are recognized. The previously taxonomically unplaced genus *Cysticapnos* Mill. (3 spp.) is included with two other monotypic native South African genera, *Discocapnos* Cham. & Schltld. and *Trigonocapnos* Schltr., in an enlarged circumscription of subtribe Discocapninae, which is morphologically defined by tendrilliferous leaves and mostly sessile racemes with the lowermost flower basal. Two subspecies are recognized in *Cysticapnos vesicaria* (E.Mey. ex Bernh.) Lidén, subsp. *vesicaria* with fewer, smaller flowers and subsp. **namaquensis** J.C.Manning & Goldblatt for plants from Namaqualand with more numerous, often larger flowers. *C. parviflora* Lidén appears to be nothing more than a dwarf-fruited form of *C. vesicaria*, in which heterocarpy has long been known. *C. pruinosa* (E.Mey. ex Bernh.) Lidén is recorded for the first time to be a short-lived perennial and not an annual, thus unique in the tribe Fumarieae. *Discocapnos mundii* var. *dregei* Harv. from the southern Cape is treated as subsp. **dregei** (Harv.) J.C.Manning & Goldblatt on account of its slightly smaller fruits and significant geographical disjunction from subsp. *mundii*. Three introduced species are included, *Fumaria capreolata* L., *F. muralis* Sond. ex W.D.Koch subsp. *muralis* and *F. parviflora* Lam. var. *parviflora*, although only the last two appear to be truly naturalized.

INTRODUCTION

Fumariaceae are a well-circumscribed family, sister to a monophyletic Papaveraceae *sensu stricto* (APG 2003). Although included in a broader circumscription of Papaveraceae by some authors, e.g. Bremer *et al.* (2003), the two groups represent reciprocally monophyletic clades that are optionally retained as separate families (APG 2003). We adopt the latter option, following Lidén (1993) as the most recent complete classification of Fumariaceae. Treating Fumariaceae in Papaveraceae as subfamily Fumarioideae has nomenclatural implications on the rank of lower-order taxa that have yet to be fully implemented.

Fumariaceae are readily distinguished from Papaveraceae by the colourless or yellow, watery or translucent (not milky) exudate, strongly zygomorphic or bilaterally symmetric flowers with small sepals, and petals that are not crumpled in bud. In addition, one or both of the outer petals are spurred basally, the stamens are usually connate into two bundles, and the bicarpellate, syncarpous ovary ripens into a capsule or nut (Bremer *et al.* 2003; Lidén 1993).

Fumariaceae are primarily north temperate, comprising 17 genera and ± 530 species. The family is taxonomically relatively well understood (Lidén 1993), and comprises the two subfamilies Fumarioideae (DC.) Endl. and Hypecoideae (Dum.) Prantl

& Kündig, the latter consisting of the single genus *Hypecoum* L. from the Mediterranean and Asia. Subfamily Fumarioideae includes the tribe Corydaleae Rchb., characterized by many-seeded capsules containing seeds with a conspicuous elaiosome, and the tribe Fumarieae, mostly with nuts or few-seeded capsules, usually a caducous style, and seeds lacking an elaiosome. The tribe Fumarieae is in turn divided into the three subtribes Sarcocapninae Lidén, Fumariinae, and Discocapninae Lidén.

The family is poorly represented in sub-Saharan Africa with just two species known from tropical Africa (Lucas 1962), *Fumaria abyssinica* Hamm. and *Corydalis mildbraedii* Fedde. Both are widely distributed from Ethiopia to Kenya and Tanzania, and represent large genera that are primarily northern hemisphere in distribution. This contrasts sharply with the situation in southern Africa, which is home to five species in three genera, all endemic to the subregion. Two of these genera, *Discocapnos* Cham. & Schltld. and *Trigonocapnos* Schltr., are monotypic and together comprise subtribe Discocapninae Lidén but the third genus *Cysticapnos* Miller (3 spp.) is not currently placed at tribal level (Lidén 1986, 1993). The subtribe Discocapninae is characterized by tendrilliferous leaves and single-seeded, pubescent achenes. *Cysticapnos* has similar tendrilliferous leaves but a many-seeded, dehiscent, capsular fruit. DNA studies (Forest & Manning in prep.) indicate that the three southern African genera, *Cysticapnos*, *Discocapnos* and *Trigonocapnos* constitute a monophyletic lineage within Fumarieae, and all three genera are thus most appropriately accommodated in an enlarged Discocapninae. The subtribe is defined morphologically by its tendrilliferous leaves, found elsewhere in the family only in the Mediterranean genus *Ceratocapnos* Dur. (tribe Fumarieae subtribe Sarcocapninae) and in

* Compton Herbarium, South African National Biodiversity Institute, Private Bag X7, 7735 Claremont, Cape Town.

** B.A. Krukoff Curator of African Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, USA.

*** Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3DS, UK.

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Dactylicapnos Wall. (tribe Corydaleae Rchb.) from the Himalayas. Several of the species also have sessile racemes (the lowermost flower arising at the base of the peduncle), whereas other genera of Fumariaceae typically have distinctly pedunculate racemes (the lowermost flower inserted well above the base of the peduncle). Anatomy of the seed coat is essentially identical in *Cysticapnos*, *Discocapnos* and *Trigonocapnos* (Fukuhara & Lidén 1995a) and also in several other genera of Fumariaceae and Corydaleae, thus offering no additional synapomorphies for the subtribe. Of potentially greater interest is the observation that *Discocapnos* and *Trigonocapnos* share an unusual vasculature of the fruit wall in which the funicular supply is ultimately derived from the ventral and dorsal bundles rather than from the lateral bundles as in other fumarioids (Fukuhara 1995; Fukuhara & Lidén 1995b). Unfortunately the pericarp vasculature of *Cysticapnos* has not been studied and it is therefore not known which pattern it follows.

The molecular analysis (Forest & Manning in prep.) retrieves *Discocapnos* as sister to *Trigonocapnos* plus a monophyletic *Cysticapnos*, with the entire clade sister to *Fumaria* L. This relationship supports the interpretation that the nutlet is plesiomorphic for the subtribe Discocapninae and that the capsules of *Cysticapnos* represent an autapomorphy for the genus. This topology offers two logical alternatives for circumscribing genera in the subtribe Discocapninae. The first retains three separate genera as circumscribed by Lidén (1986, 1993), whereas the second includes *Discocapnos* and *Trigonocapnos* within an enlarged *Cysticapnos*. The latter treatment is not consistent with the current circumscription of genera in the family (Lidén 1993), in which fruit type is extensively used as the basis for separating related genera, resulting in constellations of oligotypic genera clustered around the two large genera *Corydalis* DC. and *Fumaria*. The merits of this approach may be debated but at this stage it is unjustifiable to treat the southern African genera in a radically different way in the face of the molecular evidence that they are indeed monophyletic as currently construed. The capsular fruits of *Cysticapnos* represent a significant evolutionary innovation that in the current classification justifies its retention as a separate genus. Any changes to generic circumscriptions in the tribe Discocapninae are best done in the context of a reappraisal of the entire family. The southern African clade is adequately identified as the subtribe Disco-

capninae for purposes of biogeographic or phylogenetic investigation.

The first southern African species of Fumariaceae to be described were placed either in the genus *Corydalis* (capsular-fruited species) or *Fumaria* (those with nutlets). The varied and distinctive fruits of several of the southern African taxa, however, soon led to their taxonomic separation into distinct genera, beginning with the genus *Cysticapnos* (Miller 1754), erected for the bladder-fruited species that was until then known as *Corydalis vesicaria* L. The genus *Phacocapnos* Bernh. was later described (Bernhardi 1838) for the remaining capsular-fruited species with compressed fruits but is now included within *Cysticapnos* (Lidén 1986). The two nutlet-fruited species remain respectively in the monotypic genera *Discocapnos* (Chamisso & Schlechtendel 1826) and *Trigonocapnos* (Schlechter 1899).

The southern African Fumariaceae were first reviewed by Harvey (1894) for *Flora capensis* and later more thoroughly by Hutchinson (1921) as part of his treatise on the biogeography of the family. The most recent, and only modern revision of the southern African species, is the worldwide study of the family by Lidén (1986), in which the current generic concepts and classification were established, and the application of the names of the species was fixed. A milestone in the study of the family, this treatment is nomenclaturally incomplete and is also based on examination of very limited material of the southern African taxa, essentially the types. With more extensive material available, it is evident that two of the species recognized there, viz. *Cysticapnos grandiflora* sensu Lidén and *C. parviflora* Lidén, cannot be upheld. In addition, the patterns of geographical variation shown in both *C. vesicaria* and *Discocapnos mundii*, support the recognition of subspecies in each. We provide here a complete, illustrated account of the native species of southern African Fumariaceae, based on extensive field and herbarium study. Three introduced species of *Fumaria* that have become \pm naturalized are also included, following the taxonomy of Lidén (1986).

MATERIALS AND METHODS

This study is based on an examination of living plants in the field and of specimens in the following herbaria: BOL, K, MO, NBG, NU, PRE, TCD (acronyms as in Holmgren *et al.* 1990). The abbreviation of authors' names follows Brummitt & Powell (1992).

Key to genera of Fumariaceae in southern Africa

- 1a Leaves not tendrilliferous; racemes pedunculate; style twice or more as long as ovary, caducous; fruiting pedicels usually suberect, thickened; fruit a subglobose nutlet with woody endocarp subtribe Fumariinae: *Fumaria* (introduced species)
- 1b Terminal leaflets of some or all leaves developed into tendrils; racemes pedunculate or sessile (lowermost flower basal); style \pm as long as ovary or shorter, usually persistent; fruiting pedicels recurved, not thickened; fruit a capsule or achene, without woody endocarp subtribe Discocapninae:
- 2a Fruit a several-seeded capsule; spur on upper petal \pm as long as wide or shorter; style less than half as long as ovary, persistent 3. *Cysticapnos*
- 2b Fruit a 1-seeded, pubescent or scabridulous achene; spur on upper petal \pm twice as long as wide; style \pm as long as ovary, persistent or caducous:
- 3a Flowers and fruit with pedicels \pm 1.5 mm long; achene disciform, sparsely puberulous; style persistent 1. *Discocapnos*
- 3b Flowers and fruit with pedicels 3–4 mm long; achene obovate-trigonal, densely scabridulous; style caducous 2. *Trigonocapnos*

I. Subtribe **Discocapninae** Lidén, *Opera Botanica* 88: 104 (1986), emend. J.C.Manning & Goldblatt. Type genus: *Discocapnos* Cham. & Schldtl.

Scandent annuals or rarely perennial (one species only) with bipinnate, tendrilliferous leaves. *Racemes* pedunculate or sessile (lowermost flower basal). *Flowers* pink with purple tip, upper petal spurred, inner petals apically keeled or winged. *Style* usually persistent (rarely deciduous); stigma with two papillae. *Fruit* either a many-seeded capsule or a one-seeded achene, without a woody endocarp.

Three genera: *Cysticapnos*, *Discocapnos* and *Trigonocapnos*. Southern Africa.

1. **Discocapnos** Cham. & Schldtl., *Linnaea* 1: 569 (1826); Harv.: 18 (1894); Hutch.: 114 (1921); Lidén: 104 (1986), 316 (1993). *Fumaria* sect. *Discocapnos* (Cham. & Schldtl.) Prantl in Prantl & Kündig: 145 (1891). Type species: *D. mundii* Cham. & Schldtl.

Brittle, semi-succulent, glabrous, climbing annual; stems quadrate, with obscure unicellular papillae along angles; sap watery, yellow. *Leaves* alternate, bipinnately compound, primary divisions alternate, ultimate leaflets obovate and 3-partite; terminal leaflets of all or only upper leaves transformed into tendrils. *Inflorescence* pedunculate, terminal but leaf-opposed through rapid growth of axillary bud, racemose; bracts scale-like, petaloid, irregularly toothed. *Flowers* zygomorphic, bilabiate, pink, unscented. *Sepals* 2, lateral, much shorter than petals, scale-like, petaloid, irregularly toothed. *Petals* 4 in 2 series, outer petals larger, naviculate-spathulate, laterally winged apically, upper spurred at base, inner petals apically connate, clawed, limb inflated with dorsal crest, claw basally adnate to upper petal. *Stamens* 6, diadelphous in abaxial and adaxial bundles of 3; filaments of each bundle fused, lanceolate, membranous, clasping ovary, upper filament cluster adnate to margins of dorsal petal basally to form small chamber, with nectary decurrent on dorsal petal into spur. *Ovary* suborbicular, dorsoventrally compressed with peripheral rim, bearing unicellular papillae; ovule solitary, lateral; style short, \pm as long as ovary, flexed upwards apically, persistent; stigma compressed, 2-lobed. *Fruit* pendulous, dorsoventrally compressed, suborbicular with peripheral wing, pubescent, indehiscent and dropping entire, papery. *Seed* solitary, lenticular, glossy black, colliculate, without elaiosome.

One sp., South Africa, southwestern and southern Cape.

1.1. **Discocapnos mundii** Cham. & Schldtl. [as '*mundtii*'] in *Linnaea* 1: 569 (1826); Harv.: 18 (1894); Hutch.: 114 (1921). Lidén: 104 (1986). *Fumaria mundtii* (Cham. & Schldtl.) Prantl & Kündig: 145 (1891). Type: South Africa, Cape of Good Hope, without precise locality, August [without year], *Mund & Maire s.n.* [B-WILLD, holo.].

Climbing annual up to 1 m, with yellow sap. *Leaves* bipinnately compound, rachis flexuose, ultimate segments broadly obovate, 2- or 3-lobed almost to base, lobes elliptical to obovate, terminal segments transformed into tendrils. *Inflorescence* up to 100 mm long in fruit, 8–15-flowered; pedicels erect, apically recurved,

\pm 1.5 mm long; bracts erect, clasping pedicel, \pm 1 \times 0.5 mm, irregularly toothed. *Flowers* pale pink with dark reddish tips. *Sepals* peltate, ovate, \pm 1.0 \times 1.5 mm, irregularly toothed. *Petals*: outer petals naviculate-spathulate, 4.5–5.0 \times 1.0–1.5 mm, apically short-winged, wings patent, \pm 0.5 mm wide, upper spurred at base, spur 2.5–3.0 mm long; inner petals \pm 4 mm long, claw \pm 1.5 mm long, adnate to upper petal in lower 1 mm, blade inflated, ellipsoid, 2.5 \times 1 mm, with fleshy dorsal crest \pm 1 mm wide. *Stamens*: filament bundles lanceolate, 2.5–3.0 \times 1 mm, basal nectary decurrent up back of upper petal spur to near apex, vestigial; anthers \pm 0.25 mm long, yellow. *Ovary* discus-shaped, 2 \times 2 mm, green, minutely papillate; style maroon, flexed sharply upwards apically, \pm 1.5 mm long, persistent. *Fruit* pendent, discus-shaped with peripheral, radially costate wing, (3–)4–5 mm diam., pubescent with unicellular trichomes longest over seed-body, papery, indehiscent and dropping entire, brownish black when mature. *Seed* lenticular, (3–)4–5 mm diam., glossy black, colliculate. *Flowering time*: (August) October–December. Figure 1.

Distribution and ecology: apparently a rare species, with a discontinuous distribution along the cooler, southern foothills of the coastal mountains of the southwestern and southern Cape (Figure 2). The species has been recorded from the Cape Peninsula and adjacent mountains in the southwest, and then some 300 km to the east in the Outeniqua and Tsitsikamma Mountain ranges. *Discocapnos mundii* is restricted to moist, loamy or humic soils on the edge of forest and bush clumps, usually in sheltered valleys or drainage lines, where plants scramble among bushes and grasses. Its distribution tracks the scattered occurrence of afrotemperate forests in the southwestern and southern Cape but it is curious that the species has not been recorded from forest patches along the southern slopes of the intervening Rivieronderend or Langeberg ranges. The plants are, however, inconspicuous and easily overlooked and suitable habitats in these mountain ranges should be investigated in search of additional populations linking the two known areas of occurrence.

Diagnosis and relationships: *Discocapnos mundii* is recognized by its distinctive, discus-shaped samaras containing a solitary seed with a colliculate testa. The seeds of the other southern African species of *Fumariaceae* have scalariform-colliculate surface sculpturing. The one-seeded, indehiscent fruits with pubescent pericarp are shared with *Trigonocapnos lichtensteinii* but the trichomes in *D. mundii*, with their uniquely sculptured cuticular ornamentation (Lidén 1986), are already evident at anthesis rather than developing after fertilization, as in *T. lichtensteinii*, possibly indicating that the pericarp vestiture is independently derived in the two species. Other similarities between the two include the flexuose leaf rachis with the primary divisions of the blade alternate, unlike those of *C. cracca* and *C. vesicaria*, which are often opposite, the strongly spurred dorsal petal, and the relatively rudimentary wings on the lower petal. These characters, however, are also shared with *Fumaria* and are thus evidently ancestral conditions and thus not indicative of a sister-species relationship.

History: the species has an uncomplicated history, presumably on account of its rarity and distinctive fruits.



FIGURE 1.—*Dicocapnos mundii* subsp. *mundii*: A, portion of stem; B, lower leaf; C, flower, front and lateral views; D, lower outer petal; E, inner petals; F, androecium and section through spur; G, gynoecium, dorsal and lateral views; H, fruit; I, seed. Scale bar: A, B, 10 mm; C–G, 1 mm; H, 1.6 mm; I, 1.2 mm. Artist: John Manning.

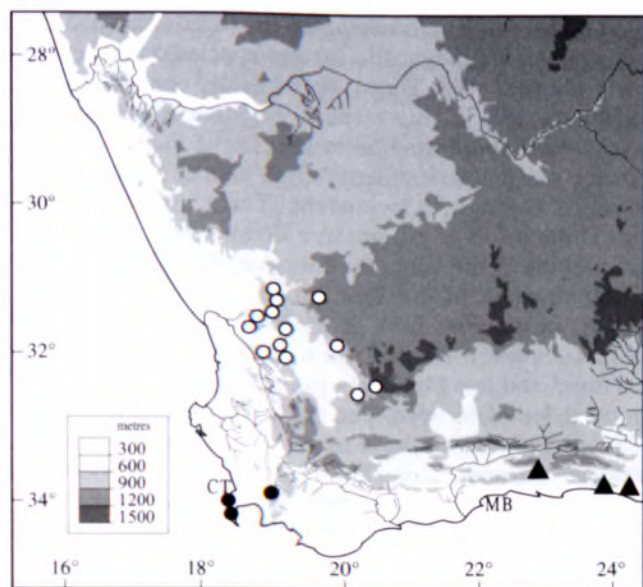


FIGURE 2.—Known distribution of *Discocapnos mundii* subsp. *mundii*, ●; *D. mundii* subsp. *dregei*, ▲; and *Trigonocapnos lichtensteinii*, ○.

It was first collected by the German pharmacist Johannes Mund, who had been despatched to the Cape in 1816 as official plant collector by the Prussian government (Gunn & Codd 1981). His fruiting collection of *Discocapnos mundii* was made in the vicinity of Cape Town, probably soon after his arrival. Mund met Chamisso in Cape Town in 1818 (Gunn & Codd 1981), who subsequently named the species for him (Chamisso & Schlechtendel 1826) in the new genus *Discocapnos* on account of its unusual disc-like fruit. It has been recognized under this name ever since. The original spelling of the epithet as *mundtii* should be treated as an orthographic error and corrected to *mundii* (McNeil *et al.* 2006: Art. 60.7) since his letters to Hooker are signed L. Mund (Gunn & Codd 1981).

Key to subspecies

- 1a Fruits mostly 4–5 mm long subsp. *mundii*
- 1b Fruits ± 3 mm long subsp. *dregei*

1.1a. subsp. **mundii**

Fruits (3.5)4–5 mm diam., with peripheral wing 0.8–1.0 mm wide.

Distribution: restricted to the southwestern Cape and mostly recorded from the Cape Peninsula, where it is best known from the lower slopes of Table Mountain between Devil’s Peak and Constantiaberg, with additional collections from the northern Hottentots Holland Mountains around Jonkershoek (Figure 2).

1.1b. subsp. **dregei** (Harv.) J.C.Manning & Goldblatt, stat. nov.

D. mundii [as *mundtii*] var. *dregei* Harv. in *Flora capensis* 1: 18 (1894). *D. dregei* (Harv.) Hutch.: 114 (1921). Type: South Africa, [Western Cape], Knysna, Bosch River, between the bush and the river, October 1839, Drège s.n. (TCD, holo.!, K, S, iso.!).

Fumaria scandens E.Mey.: 125, 186 (1844), nom. nud.

Fruits 3.0–3.5 mm diam., with peripheral wing 0.5–0.8 mm wide.

Distribution: known from three collections along the southern foothills of the Outeniqua and Tsitsikamma Mountains, between Knysna and Humansdorp (Figure 2).

Distinguished from the typical subspecies by its slightly smaller fruits, 3.0–3.5 mm diam., with narrower wing less than 1 mm wide.

History: this taxon is based on a collection made near Knysna by the German botanical collector Johann Drège in October 1839. Ernst Meyer, who wrote the botanical accounts of Drège’s collections, intended to describe the species as *Fumaria scandens*, and this name appears on the TCD sheet but was never published beyond its appearance in Drège’s *Zwei pflanzengeographische Dokumente* (1844). The smaller fruits of these plants compared with those of the typical forms from the Cape Peninsula led Harvey (1894) to distinguish them as the variety *dregei*, which he further defined by its more floriferous racemes. The taxon was subsequently recognized as a distinct species by the British botanist John Hutchinson (1921) in his account of the family. Further collections of the typical form show that there are no differences in floral characters between the two sets of populations. The difference in fruit size did not impress Lidén (1986), who treated them as comprising a single entity, and indeed there are apparently no significant floral or vegetative differences between the two sets of populations. A subsequent collection of var. *dregei* from Clarkson (*Thode s.n.* BOL) confirms that the eastern populations are consistently smaller-fruited but the size difference between the two sets of populations is slight, and a plant from Jonkershoek (*Levy’s 8511* BOL) bears occasional fruits of 3.5 mm diam. among the more typical larger fruits of 4 mm diam. The slight but consistent difference in average size of the fruits between the western and eastern populations, combined with the significant disjunction between them, supports taxonomic recognition at some level, and we treat them as subspecies.

2. **Trigonocapnos** Schltr. in *Botanische Jahrbücher* 27: 131 (1899); Hutch.: 113 (1921); Lidén: 105 (1986), 316 (1993). Type species: *T. curvipes* Schltr. [= *T. lichtensteinii* (Cham. & Schldl.) Lidén].

Brittle, semi-succulent, glabrous, climbing annual; stems quadrate, with obscure unicellular papillae along angles; sap watery, yellow. *Leaves* alternate, bipinnately compound, primary divisions alternate; ultimate leaflets obovate and 3-partite; terminal leaflets of all or only upper leaves transformed into tendrils. *Inflorescence* shortly pedunculate or sessile, terminal but leaf-opposed through rapid growth of axillary bud, racemose; bracts scale-like, petaloid, irregularly toothed. *Flowers* zygomorphic, bilabiate, pink, unscented. *Sepals* 2, lateral, much shorter than petals, scale-like, petaloid, irregularly toothed. *Petals* 4 in 2 series, outer petals larger, naviculate-spathulate, laterally winged apically, upper spurred at base, inner petals apically connate, clawed, limb inflated with dorsal crest, claw basally adnate to upper petal. *Stamens* 6, diadelphous in abaxial and adaxial bundles of 3; filaments of each bundle fused, lanceolate, membranous, clasping ovary, upper filament cluster adnate to margins of dorsal petal basally to form small chamber, with vestigial nectary decurrent on dorsal petal into spur. *Ovary* obovoid with peripheral rim, concave

abaxially, bearing unicellular papillae; ovule solitary, sub-basal; style short, \pm as long as ovary, flexed upwards apically, deciduous; stigma compressed, 2-lobed. *Fruit* pendulous, dorsally crested with lateral rims folded downwards, thus abaxially conduplicate, puberulous, indehiscent and dropping entire, leathery. *Seed* solitary, narrowly obovoid, yellowish brown, scalariform-colliculate, without elaiosome.

One sp., South Africa, northwestern parts of winter rainfall region.

2.1. ***Trigonocapnos lichtensteinii*** (Cham. & Schldl.) Lidén in *Opera Botanica* 88: 105 (1986). *Fumaria lichtensteinii* Cham. & Schldl.: 568 (1826). Type: South Africa, [Western Cape], Cape of Good Hope, without precise locality or date, *Lichtenstein s.n.* (B-WILLD12938, holo.!).

T. curvipes Schltr.: 131 (1899); Hutch.: 113 (1921). Type: South Africa, [Western Cape], Clanwilliam, 21 August 1896, R. Schlechter 8585 (BOL, lecto.!, here designated; S, iso.).

F. capreolata $\beta?$ *burchellii* DC: 130 (1824), name without rank. Type: South Africa, Karoo [Roggeveld], 1 August 1811, Burchell 1298 (not located at B, BM, K or P).

F. eckloniana Sond. in Harv.: 18 (1894), nom. nud.

F. micrantha Licht. ms. *Lichtenstein s.n.* (B-WILLD12938).

Climbing annual up to 1 m, with yellow sap. *Leaves* bipinnately compound, rachis flexuous, ultimate segments broadly obovate, 2- or 3-lobed to base, lobes elliptical, terminal segments transformed into tendrils. *Inflorescence* up to 70 mm long in fruit, 20–40-flowered; pedicels suberect, apically recurved, 3–4 mm long; bracts erect, clasping pedicel, 1.0–1.5 \times 0.5 mm, irregularly toothed. *Flowers* pale pink with dark purple tips. *Sepals* peltate, ovate, \pm 0.5 mm long, irregularly toothed. *Petals*: outer petals naviculate-spathulate, 2.5–3.0 \times 0.5–1.0 mm, apically short-winged, wings patent, \pm 0.5 mm wide, upper spurred at base, spur 2.0–2.5 mm long; inner petals \pm 3 mm long, claw \pm 1.5 mm long, adnate to upper petal in lower 1 mm, blade inflated, ellipsoid, 1 \times 0.75 mm, with fleshy dorsal crest \pm 0.75 mm wide. *Stamens*: filament bundles oblong, 1.5–2.0 \times 1 mm, basal nectary decurrent up back of upper petal spur to near apex, vestigial; anthers \pm 0.1 mm long, yellow. *Ovary* obovoid with peripheral rim, concave beneath, 1 \times 0.5 mm, green, colliculate; style translucent, flexed sharply upwards apically, \pm 1 mm long, basally constricted, deciduous. *Fruit* pendent, obovoid-trigonous, dorsally crested with lateral rims folded downwards, thus abaxially conduplicate, 3 mm long, 1.5 mm high and 1.0 mm wide, puberulous, indehiscent and dropping entire, brown when mature, leathery. *Seed* narrowly obovoid, 2 \times 1 mm, yellowish brown, scalariform-colliculate. *Flowering time*: August–September. Figure 3.

Distribution and ecology: *Trigonocapnos lichtensteinii* occurs along the Bokkeveld–Matsikamma Escarpment southwards through the northern Cedarberg to Clanwilliam, and inland from the foot of the Hantamsberg at Calvinia along the Roggeveld Escarpment as far south as the Koedoesberg at the northwestern edge of the Klein Roggeveld (Figure 2). Plants grow in sheltered, seasonally moist situations, along drainage lines or at the base of rocky outcrops in fine-grained clay soils, where they clamber among the surrounding shrubbery.

Diagnosis and relationships: the tricostate, puberulous achenes are diagnostic for the species, as is the narrowly obovoid seed. The style is basally constricted and deciduous, and in this respect *Trigonocapnos lichtensteinii* more closely resembles species of *Fumaria* rather than the indigenous southern Africa taxa of Fumariaceae, in which the style is persistent. The curiously shaped fruit is the result of progressive downward curvature of the margins of the ventrally concave, disc-shaped ovary during ripening of the fruit. In its puberulous, single-seeded, indehiscent fruit, *T. lichtensteinii* most resembles *Discocapnos mundii*, but in that species the fruit is disciform and less obviously puberulous, and contains a rounded, lenticular seed. The trichomes on the fruit of *T. lichtensteinii*, unlike those of *D. mundii*, are lacking in cuticular ornamentation (Lidén 1986) and only develop after anthesis, suggesting that pubescence in the two species may have been independently derived. Other similarities between the two species, notably their flexuous leaves with alternate primary segments, and their strongly spurred flowers with rudimentary apical wings on the outer petals, appear to be ancestral and thus not indicative of a sister-species relationship.

History: the species was first collected sometime in the early years of the nineteenth century by Martin Heinrich Lichtenstein, a German physician and naturalist who accompanied the incumbent Governor of the Cape of Good Hope, J.W. Janssens, as family physician on his arrival in Cape Town at the end of 1802 (Gunn & Codd 1981). Over the next three years, Lichtenstein made three journeys into the interior of the country, all of which passed through the Klein Roggeveld, where he almost certainly collected *Trigonocapnos lichtensteinii*. Although Lichtenstein intended to describe his collection under the name *Fumaria micrantha*, this manuscript name remained unpublished and the species was only formally described more than two decades later, when it was named for him by the German botanists Ludolf von Chamisso and Diederich von Schlechtendal (1826).

The next collection of the species was also made during a journey up to the Roggeveld Escarpment, this time by the English explorer William Burchell on 1 August 1811, who noted in his *Travels in the interior of southern Africa* of 1822 (Burchell 1953: 174) that among the 14 specimens collected that day 'was a Fumitory so exceedingly like an English species, as hardly to be distinguished from it'. This opinion was evidently shared by Alphonse de Candolle (1824), who distinguished Burchell's plant only as a form of the European *Fumaria capreolata*, basing his identification on the recurved pedicels that characterize the latter species. Although seen by de Candolle in Burchell's herbarium, we have been unable to locate this specimen but the description of the cirrhose leaves and relatively long, recurved fruiting pedicels (de Candolle 1824: 130) can only apply to *Trigonocapnos lichtensteinii* among the South African taxa and this, combined with the locality, make its identification certain. The species remained poorly known and Harvey (1894: 18) in his account of the family for *Flora capensis*, following the advice of Sonder, included it in the European species *F. muralis*, as yet another of the multiplicity of 'book species' of this variable taxon that so aggravated him.



FIGURE 3.—*Trigonocapnos lichtensteinitii*: A, portion of stem; B, flower, front and lateral views; C, lower outer petal; D, inner petals; E, gynoecium, dorsal, lateral and partial ventral views, style removed; F, immature fruit, lateral and front views; G, mature fruit, front, lateral and three-quarter views; H, seed. Scale bar: A, 10 mm; B–E, G, 1 mm; F, 0.5 mm; H, 0.25 mm. Artist: John Manning.

It is little wonder, therefore, that it was subsequently re-described as a distinct genus by the German botanist Rudolph Schlechter (1899) from a collection that he had made a few years earlier in the Pakhuis Mountains. This is the name under which the species remained known until Lidén (1986) recognized that Chamisso and Schlechtendal's name took priority and accordingly effected its transfer to *Trigonocapnos*. The species is now relatively well known from the Bokkeveld and Pakhuis Mountains but has only been sporadically collected from the Roggeveld and Klein Roggeveld Escarpments.

3. *Cysticapnos* Mill., The gardener's dictionary (1754); Harv.: 16 (1894); Hutch.: 110 (1921); Fedde: 286 (1924); Lidén: 105 (1986), 316 (1993). Type species: *C. vesicaria* (L.) Fedde.

Phacocapnos Bernh.: 664 (1838); Hutch.: 109 (1921). *Corydalis* sect. *Phacocapnos* (Bernh.) Prantl in Prantl & Kündig: 144 (1889); Harv.: 16 (1894). Type species: *P. cracca* (Cham. & Schltl.) Bernh.

Brittle, semi-succulent, glabrous, climbing annuals with slender taproot or rarely (*C. pruinosa*) perennial with fleshy taproot; stems quadrate, with obscure unicellular papillae along angles; sap watery, clear or yellow. *Leaves* alternate, pinnately or bipinnately compound, primary divisions alternate or opposite; ultimate leaflets elliptical or obovate-cuneate and deeply 3-lobed; terminal leaflets of all or only upper leaves transformed into tendrils. *Inflorescence* pedunculate or sessile, terminal but leaf-opposed through rapid growth of axillary bud,

racemose; bracts scale-like, petaloid, irregularly toothed. *Flowers* zygomorphic, bilabiate, pink, unscented. *Sepals* 2, lateral, much shorter than petals, scale-like, petaloid, irregularly toothed. *Petals* 4 in 2 series, outer petals larger, naviculate-spathulate, laterally expanded or winged apically, upper saccate or short-spurred at base, inner petals apically connate, clawed, limb inflated with dorsal crest, claw basally adnate to upper petal. *Stamens* 6, diadelphous in abaxial and adaxial bundles of 3; filaments of each bundle fused, lanceolate, membranous, clasping ovary, upper filament cluster adnate to margins of dorsal petal basally to form small chamber, with nectary basal or decurrent on dorsal petal into spur, pulvinate. *Ovary* ovoid, sometimes dorsoventrally compressed, glabrous; ovules several in 2–several series on lateral placentas; style short, straight or geniculate; stigma compressed, 2-lobed. *Fruit* pendulous, capsular, papery, sometimes inflated and bladder-like, circumferentially partially or completely dehiscent. *Seeds* several, lenticular, glossy black, testa obscurely scalariform-colliculate or almost smooth.

Three spp., temperate South Africa, southern Namibia and Lesotho, winter rainfall region and along eastern escarpment to Mpumalanga.

Key to species

- 1a Perennial with fleshy taproot; leaves finely divided, carrot-like; racemes pedunculate, mostly 14–35-flowered; inner petal crests papillate; nectary adnate to lower half of spur; capsules lanceolate-quadrate, transversely flexed 3.2 *C. pruinosa*
- 1b Annuals with slender taproot; leaves not finely divided, *Aquilegia*-like, ultimate segments elliptic; racemes sessile (lowermost flower basal), 1–15(–20)-flowered; inner petal crests smooth; nectary at base of staminal sheath, not adnate to spur; capsules not transversely flexed:
- 2a Raceme 4–15(–20)-flowered; ± 1 mm long, pedicels shorter than bracts; outer petal wings small, ± 1 mm wide, not extending apically; capsule flattened, lanceolate, 5–12 mm long; style straight; sap yellow 3.1 *C. cracca*
- 2b Raceme (1)2–7-flowered; pedicels 2–8 mm long, longer than bracts; outer petal wings large, 2–4 mm wide, encircling petal apices; capsule ovoid, usually inflated, 20–25 mm long, rarely dwarfed, 4–10 mm long; style sharply sigmoid at base; sap clear 3.3 *C. vesicaria*

3.1. ***Cysticapnos cracca*** (Cham. & Schltld.) Lidén in *Opera Botanica* 88: 108 (1986). *Corydalis cracca* Cham. & Schltld.: 567 (1826); Harv.: 17 (1894). *Phacocapnos cracca* (Cham. & Schltld.) Bernh.: 664 (1838); Hutch.: 110 (1921). Type: South Africa, [Western Cape], Cape of Good Hope, without precise locality or date, *Bergius s.n.* (S, holo.).

Phacocapnos dregeanus Bernh.: 664 (1838). Type: South Africa, [Western Cape], Enon, White River, 11 November 1829, *Drège 7586* (MO, holo.!; PRE, iso.!).

Corydalis laevigata E.Mey.: 95, 125 (1844), nom. nud.

Climbing annual up to 1 m, with yellow sap. *Leaves* bipinnately compound, ultimate segments broadly obovate, 2- or 3-lobed almost to base, lobes elliptical to obovate, terminal segments transformed into tendrils. *Inflorescence* sessile with lowest flower basal, up to 80 mm long in fruit, 4–15(–20)-flowered; pedicels suberect and slightly curved outwards, ± 1 mm long; bracts recurved, lanceolate, 1.5–2.0 \times 0.5–0.75 mm, irregularly toothed. *Flowers* pale pink with dark reddish tips. *Sepals* ovate, 1.0–1.5 \times 0.5–0.75 mm, irregularly toothed. *Pet-*

als: outer petals naviculate-spathulate, 6.0–6.5 \times 1.5–2.0 mm, apically winged, wings reflexed, ± 1 mm wide, upper saccate at base, sac ± 1 mm deep; inner petals 5–6 mm long, claw ± 3 mm long, adnate to upper petal in lower 1 mm, blade inflated, ellipsoid, 2–3 \times 1 mm, with fleshy dorsal crest ± 1 mm wide. *Stamens*: filament bundles lanceolate, 4.0–4.5 \times 1 mm, upper bundle adnate to upper petal along margins in lower 3 mm, nectary basal, pulvinate; anthers ± 0.25 mm long, yellow. *Ovary* dorsoventrally flattened, lanceolate, 4 \times 2 mm, green, sparsely and obscurely papillate; style straight or slightly curved, ± 1 mm long; ovules biseriate, ± 8 per placenta. *Fruit* pendent, dorsoventrally compressed, lanceolate, (5–)9–12 \times 2–3 mm, dehiscent from base to \pm halfway, remaining attached to replum (placenta) in distal half, several-seeded. *Seeds* lenticular, 0.6–0.8 mm diam., glossy black, obscurely scalariform-colliculate. $2n = \pm 32$ (Lidén 1986). *Flowering time*: (August) September to October. Figure 4.

Distribution and habitat: occurs among bushes in seasonally moist, sheltered situations in coastal and inland scrub up to ± 1 000 m, from the Bokkeveld Escarpment through the southwestern and southern Cape and into the Eastern Cape as far as Port Elizabeth, Port Alfred and Grahamstown (Figure 5). The species usually grows in fine-grained clay or loamy, granite-derived soils but sometimes in neutral sands, often on south-facing slopes that are shaded in the afternoon. On nutrient-poor sandstone soils plants have been recorded as favouring richer, nitrified hyrax middens.

Diagnosis and relationships: *Cysticapnos cracca* is recognized by its lanceolate, blade-like capsules, 10–12 \times 2–3 mm, containing numerous seeds in two peripheral rows. The pericarp dehisces from the base, with the two halves peeling away but remaining attached in the distal half. In general form and dehiscence they are very similar to those of *C. pruinosa*, but the latter has larger, \pm quadrate capsules, 15–17 mm long, that are distinctly flexed upwards in the distal half, with obscurely scalloped margins. The racemes in *C. cracca* are almost invariably sessile, with flowers smaller than those of *C. pruinosa* (6.0–6.5 mm vs 7–8 mm) and generally fewer per raceme (mostly up to 15 vs more than 15). Vegetatively *C. cracca* is readily distinguished from *C. pruinosa* by its annual habit, less finely divided leaves, and yellow vs clear sap.

Cysticapnos cracca is most likely to be confused with *C. vesicaria*, with which it co-occurs in parts of the southwestern Cape. Although typically smaller and more compact than *C. vesicaria*, *C. cracca* is otherwise almost indistinguishable in foliage, both species having broadly obovate, deeply 2- or 3-lobed ultimate leaf segments. The sap of *C. cracca*, however, is distinctly yellow, staining the skin bright orange, whereas that of *C. vesicaria* is clear. The two species are readily distinguished in flower and fruit, *C. cracca* having smaller, less prominently winged flowers and flattened, non-inflated capsules. Although *C. cracca* is typically found in heavier, clay soils, with *C. vesicaria* favouring deep coastal sands and gritty granite-derived soils, the two species have been recorded growing together in several places throughout their area of sympatry.

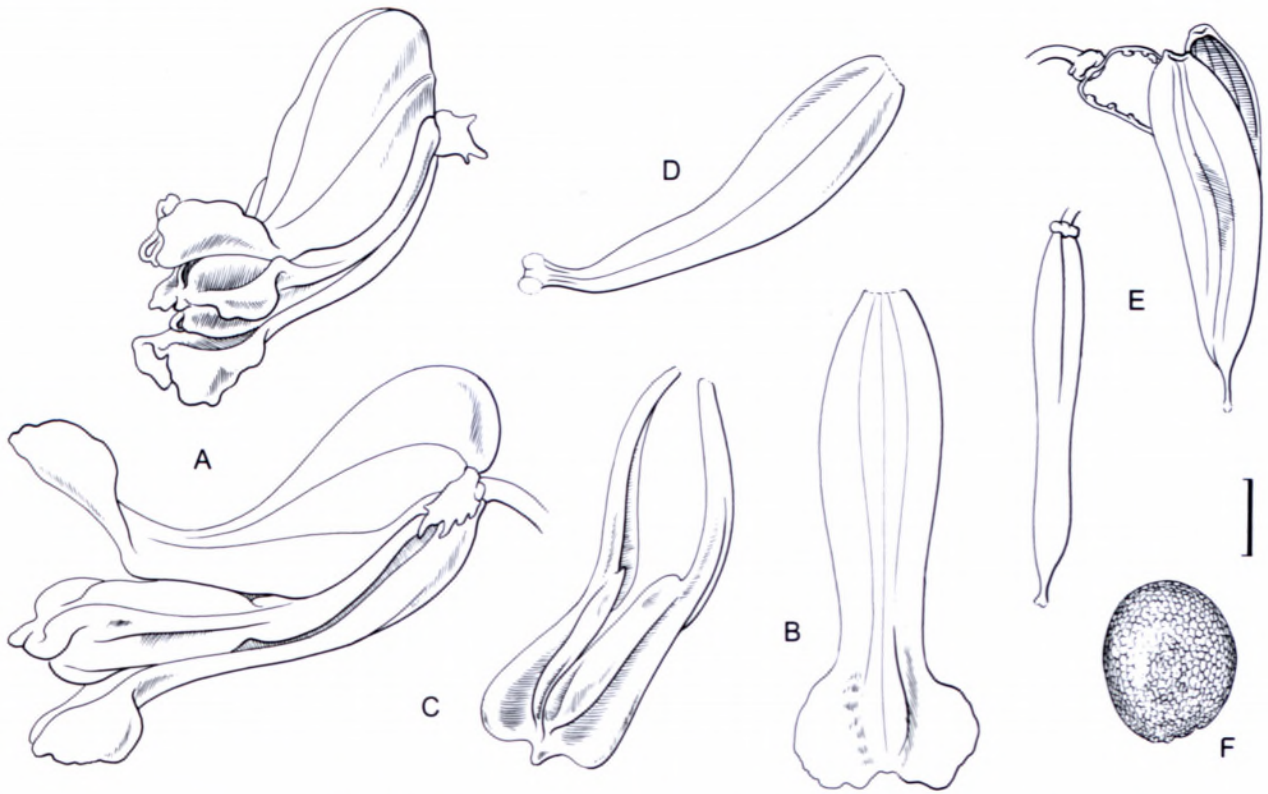


FIGURE 4.—*Cysticapnos cracca*: A, flower, front and lateral views; B, lower outer petal; C, inner petals; D, gynoecium, lateral view; E, mature fruit, lateral view before dehiscence and dorsal view after dehiscence; F, seed. Scale bar: A–C, 10 mm; E, 2.5 mm; F, 0.4 mm. Artist: John Manning.

History: *Cysticapnos cracca* was first collected by the German apothecary Carl Bergius, who arrived at the Cape in 1815. He almost certainly gathered the specimens in the immediate surrounds of Cape Town itself, and as he died here a few years later, at the beginning of 1818 (Gunn & Codd 1981), his collection must date from this three-year period. The species was described several years later in the genus *Corydalis* by the German botanists Ludolf von Chamisso and Diederich von Schlechtendal (1826) but was later transferred by Bernhardt (1838) to his new genus *Phacocapnos*, which he distinguished from *Corydalis* primarily on the lack of an aril or strophiole on the seed. This treatment was not followed by Harvey (1894) but was adopted by later botanists. At the same time Bernhardt (1838) described a later collection from Enon, north of Port Elizabeth, made by the German collector Johann Drège in 1828 as the new species *P. dregeanus* on the basis of its acute rather than obtuse fruits. As subsequently concluded by Harvey, this purported difference is not significant.

3.2. *Cysticapnos pruinosa* (E.Mey. ex Bernh.) Lidén in *Opera Botanica* 88: 106 (1986). *Phacocapnos pruinosa* [as *pruinosa*] E.Mey. ex Bernh.: 664 (1838); Hutch.: 110 (1921). *Corydalis pruinosa* (E.Mey. ex Bernh.) Harv.: 17 (1894). Type: South Africa, [Eastern Cape], 3027 (Lady Grey): Witberg [Witteberge], (-DA), 4000'–5000' [1 200–1 500 m], November without year [1832], Drège 3846 133 (*I. a*) (MO, holo.!, B!, BOL!, PRE!, S, iso.).

Tufted perennial with fleshy taproot, and climbing stems up to 1 m, with clear sap. *Leaves* bipinnately compound, ultimate segments broadly obovate, 2- or 3-lobed almost to base; terminal segments of upper leaves trans-

formed into tendrils. *Inflorescence* pedunculate, up to 160 mm long in fruit, 14–35-flowered, sometimes bearing 1 or 2 reduced leaves below; pedicels suberect and slightly curved outwards, 1–2 mm long; bracts recurved, lanceolate, 1.5–2.0 × 0.5–0.75 mm, irregularly toothed. *Flowers* pale pink with dark reddish green gibbae. *Sepals* ovate, 2 × 1.5 mm, irregularly toothed, basally auriculate. *Petals*: outer petals naviculate-spathulate, prominently clawed, 7–8 × 0.8–1.0 mm, apically winged and 3–4 mm wide, wings patent, ± 1.5 mm wide, upper saccate at base, sac 3–4 mm deep; inner petals 5–6 mm long, claw ± 2 mm long, adnate to upper petal in lower 1 mm, blade inflated, ellipsoid, 3–4 × 1.5 mm, with papillate dorsal crest ± 1 mm wide. *Stamens*: filament bundles lanceolate, 3.5–4.0 × 1.2 mm, upper bundle adnate to

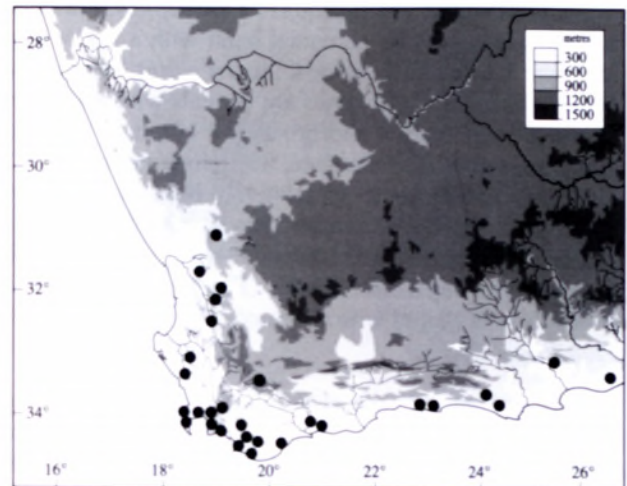


FIGURE 5.—Known distribution of *Cysticapnos cracca*.

upper petal along margins in lower 1 mm, nectary elongate-pulvinate, decurrent up lower half of spur; anthers ± 0.25 mm long, yellow. *Ovary* dorsoventrally flattened, lanceolate-quadrate, 4×1.2 mm, green; style straight, suberect, ± 0.7 mm long; ovules biseriate, ± 9 per placenta. *Fruit* pendent, dorsoventrally compressed, lanceolate-quadrate, $(12-15-25) \times 6-7$ mm, flexed upwards in distal half, margins obscurely scalloped-dentate at maturity, dehiscing from base to \pm halfway, remaining attached to replum (placenta) in distal half, many-seeded. *Seeds* lenticular, 1.0–1.5 mm diam., glossy black, scalariform-colliculate peripherally. $2n = \pm 32$ (Lidén 1986). *Flowering time*: December to February. Figure 6.

Distribution and ecology: a montane and subalpine species, distributed along the eastern escarpment of South Africa between 1 200 and 3 000 m, from the Koueveldberge west of Graaff-Reinet northwards through the Drakensberg Mountains of Eastern Cape and KwaZulu-Natal to Harrismith and westwards across the higher-lying parts of Lesotho to the Leribe Plateau (Figure 7), with isolated northern outliers along the eastern escarpment in Mpumalanga around Wakkerstroom and Ermelo and on the Mauchsberg near Lydenburg. *Cysticapnos pruinosa* typically grows in gritty, basaltic soils, scrambling among bushes and grasses on mountain slopes and in scree, in rocky boulder beds in drainage lines, or along mountain streams. It is the only member of the tribe Discocapninae to occur in the summer rainfall region.

The species has previously been regarded as an annual but excavation of several individuals confirms that it is perennial. Seedlings form the characteristic fleshy taproot within their first year but appear to flower only from the second season. Older plants develop a taproot several millimetres in diameter, and produce a crown with multiple growing points, from which new shoots arise. These, like the seedlings, seem not to flower in their first season, accumulating old leaf bases along the subterranean portion. Plants die down in winter to the crown and resprout in the spring.

The species is used medicinally by the Sotho, among whom it is known colloquially as *Musa pelo oa noka* (the river comforter), literally 'the one who puts the heart (of the river) right'. It is taken as a relief for sorrow, especially in times of bereavement (Dieterlen 873).

Diagnosis and relationships: *Cysticapnos pruinosa* is distinguished by its perennial habit with a fleshy taproot, and by its finely divided, almost carrot-like leaves. Other species of *Cysticapnos* are annuals with a slender, almost fibrous taproot and broader, \pm elliptical ultimate leaflet segments. The elongate, floriferous racemes of *C. pruinosa* produce up to 35 relatively large flowers, 7–8 mm long, with papillate rather than smooth dorsal crests on the lateral petals, and lanceolate-quadrate fruits with a distinctive transverse flexure. The clear, rather than yellow, sap is shared with *C. cracca* and with species of *Fumaria*.

History: one of several South African Fumariaceae collected by the German plant hunter Johan Drège, the species is based on his collection from the mountains around Lady Grey in Eastern Cape. Although the collection is undated as to year, his itinerary indicates that

he was in this area in late 1832 and early 1833 (Gunn & Codd 1981). Ernst Meyer, the German botanist who dealt with Drège's collections, intended describing the species in the genus *Corydalis* but his name remained unpublished and it was left to Bernhardt to formally describe the species in his new genus *Phacocapnos*, which he distinguished from *Corydalis* by the lack of an aril or strophiole on the seeds. The Bernhardt herbarium formed the basis for the Missouri Botanical Garden herbarium and the specimen there, which is marked as part of the Bernhardt Herbarium, is thus appropriately recognized as the holotype.

3.3. *Cysticapnos vesicaria* (L.) Fedde in Repertorium specierum novarum regni vegetabilis 19: 287 (1924); Lidén: 106 (1986). *Corydalis vesicaria* (L.) Pers.: 269 (1806). *Fumaria vesicaria* L.: 701 (1753). Type: South Africa, without locality or date, LINN881.16 (LINN, holo!).

C. cirrhosa Moench: 52 (1794), nom. illeg. superfl. a *Fumaria vesicaria* L.

Climbing annual up to 2 m, with clear sap. *Leaves* bipinnately compound, ultimate segments broadly obovate, 2- or 3-lobed almost to base, lobes narrowly elliptical to obovate; terminal segments transformed into tendrils. *Inflorescence* sessile (lowest flower basal), 10–60(–80) mm long, (1)2–7-flowered; pedicels suberect, curved outwards apically, 2–8 mm long, elongating to 25 mm in fruit; bracts spreading, obovate-cuneate, 2.0–2.5 \times 1.0–1.5 mm, apically toothed. *Flowers* pale pink, upper petal with dark reddish mark at base of wing, inner petals translucent. *Sepals* sagittate, 1–2(–3) \times 0.5–1.0(–2.0) mm, irregularly toothed. *Petals*: outer petals naviculate-spathulate, 7–9(–13) \times 2–3 mm, winged in outer half, wings reflexed, 2–4(–5) mm wide, upper petal rounded at base; inner petals 6–7 mm long, claw 1.5–2.0 mm long, adnate to upper petal in lower 1 mm, blade ellipsoid, inflated, 4.5–5.0 \times 1 mm, with inflated dorsal crest 1.5–2.0 mm wide. *Stamens*: filament bundles broadly lanceolate, 3.5–4.0 \times 1.5 mm, upper bundle adnate to upper petal along margins in lower 1 mm, nectary basal, pulvinate; anthers ± 0.25 mm long, yellow. *Ovary* ovoid, 3 \times 1.5 mm, green; style geniculate-sigmoid, ± 0.5 mm long; ovules 4-seriate, 30–40 per placenta. *Fruit* pendulous on elongated pedicel, heterocarpic, ovoid, usually inflated and (10–)20–25 \times (5–)15–20 mm, sometimes compressed and not inflated, then 4–10 \times 3–5 mm, exocarp splitting longitudinally for entire length, mesocarp usually aerenchymatous, endocarp remaining attached to exocarp by radiating threads, rupturing irregularly, many-seeded, rarely mesocarp not developing and fruits then much smaller, 5–10 \times 4–5 mm. *Seeds* lenticular, 1.0–1.5 \times 0.8–1.3 mm diam., excavated on faces, glossy black, obscurely colliculate and almost smooth. $2n = 28, \pm 30$ (Lidén 1986). *Flowering time*: mainly August to early October but as early as June in the Little Karoo. Figure 8.

Distribution and ecology: common and widely distributed from southern Namibia through Namaqualand and the southwestern Cape to the Little Karoo around Oudtshoorn but apparently absent from the Knersvlakte (Figure 9). The species usually occurs in coarse-grained soils, mainly coastal sands in fynbos and coastal scrub or gritty, granitic soils in renosterveld.



FIGURE 6.—*Cysticapnos pruinosus*: A, portion of flowering stem; B, base of plant; C, infructescence; D, flower, front and lateral views; E, section through spur; F, lower outer petal; G, inner petals; H, gynoecium, lateral and three-quarter views; I, seed. Scale bar: A–C, 10 mm; D–G, 1 mm; H, 0.5 mm. Artist: John Manning.

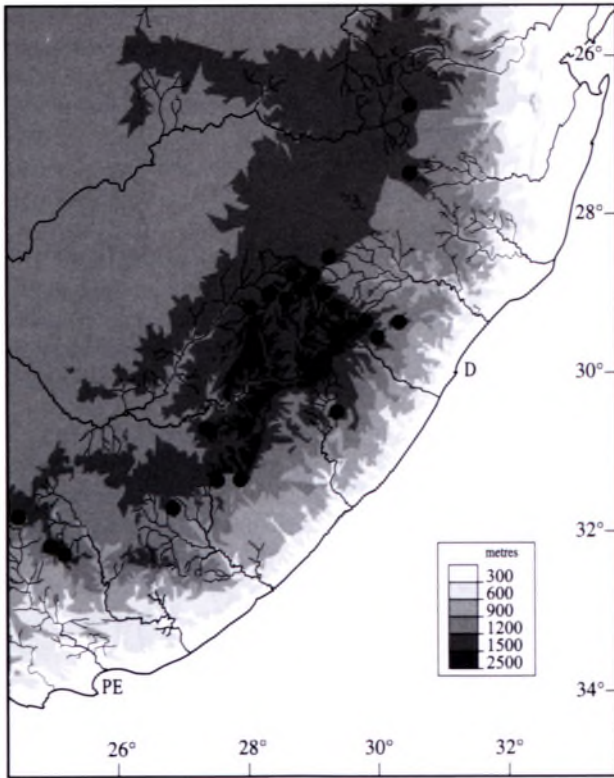


FIGURE 7.—Known distribution of *Cysticapnos pruinosa*.

Diagnosis and relationships: although similar to *Cysticapnos cracca* in foliage, *C. vesicaria* is distinguished from this and other species by the basally geniculate style and by its \pm inflated, bladder-like fruit, mostly 20–25 \times 15–20 mm. This unique fruit results from the development of a thick, highly aerenchymatous, spongy mesocarp between the papery exo- and endocarps. Even at flowering the ovary wall is clearly 3-layered. At maturity the exocarp splits longitudinally but remains attached to the endocarp by the radiating, thread-like vascular bundles, and the seeds are released through irregular rupturing of the endocarp. In some fruits, however, the mesocarp fails to expand and the capsules remain small and compressed, measuring just 4–10 \times 3–5 mm. The seeds in these small capsules are quite normal and the same plant may produce both dwarf and normal fruits. These flattened capsules are strikingly similar to those of *C. cracca* and *C. pruinosa*. The clear, watery sap is shared with *C. pruinosa*.

Heterocarpy in *Cysticapnos vesicaria* was first noticed and reported by Fedde (1924), and later by Hilliard & Burt, who recorded that 'small fruits, not inflated but with ripe seeds, [are] sometimes present on [the] same raceme [as normal inflated fruits]' (Hilliard & Burt 13025, NU). Dwarf, flattened fruits have been recorded throughout the range of the species and are a regular feature of the species. They have no taxonomic significance although they have caused confusion in the past. *Corydalis burmannii* Eckl. & Zeyh. ex Harv. was based on plants with such dwarf fruits, and a cultivated plant that produced a single dwarf fruit formed the basis of *Cysticapnos parviflora* Lidén.

The species is typically few-flowered, with 1–4 flowers borne on short racemes up to 45 mm long. The flowers are mostly 7–8 mm long, with the upper and lower

petal wings 2–3 mm wide. Populations from the northern part of the range, in Namaqualand and the Richtersveld, however, have up to seven, mostly larger flowers borne in racemes 20–80 mm long. In these plants the outer petals may reach 10–12 mm long with apical crests 3–5 mm wide. These northern forms are treated here as subsp. *namaquensis*.

History: the first of the southern African Fumariaceae to be named, *Cysticapnos vesicaria* was described in the genus *Fumaria* by Carl Linnaeus (1753). The identity of the original collector is not known but the species was soon in cultivation in Europe and became known to later botanists under the name *Cysticapnos africana*, based on an illustration of the very distinctive fruit reproduced in Gaertner's (1791) *De fructibus et seminibus plantarum*. It was only in the early decades of the twentieth century that Fedde (1924) resuscitated the use of the earlier name, *C. vesicaria*, in an article in which he first identified the existence of marked heterocarpy in the taxon. This led him to suspect that Harvey's (1894) *Corydalis burmannii* was nothing more than a smaller-fruited form of *C. vesicaria*, an opinion that has now been vindicated by further observations of plants in the field. This small-fruited form was still recognized by Lidén (1986) under the illegitimate name *Cysticapnos grandiflora*. The various forms of *C. vesicaria* distinguished by Fedde (1924) on the basis of the size of the leaf segments and flowers represent nothing more than the normal variation in leaf and floral development evident even within individuals in the same population.

Plants thought to have originated from Alexandria in Egypt were cultivated in Europe under the unpublished name *Cysticapnos alexandrina*. Although thought by Fedde (1924) to have been validated by Don, this is not in fact the case as Don (1831) indicated quite clearly his opinion that the plants in question were not distinct from *C. africana*, and the name thus remains invalid (McNeil *et al.* 2006: Art 34:1).

Key to subspecies

- 1a Raceme 10–20(–45) mm long, 1–4-flowered; outer petals 7–9 mm long with wings 2–3 mm wide; plants from southwestern and southern Cape subsp. *vesicaria*
 1b Raceme (20–)30–80 mm long, 3–7-flowered; outer petals 9–13 mm long with wings 3–5 mm wide; plants from Namaqualand and southern Namibia. subsp. *namaquensis*

3.3a. subsp. *vesicaria*

Cysticapnos africana Gaertner, *De fructibus et seminibus plantarum* 2: 161 (1791); Harv.: 16 (1894); Hutch.: 110 (1921). Type: Gaertner: 161, t. 115 (1791), icono.!

Corydalis burmannii Eckl. & Zeyh. ex Harv.: 17 (1894). *Phacocapnos burmannii* (Eckl. & Zeyh. ex Harv.) Hutch.: 110 (1921). Type: South Africa, [Western Cape], Saldanha Bay and near Brackfontein, Clanwilliam, Ecklon & Zeyher 23 (SAM, lecto.!, designated by Goldblatt & Manning (2000); B!, MO!, iso.).

Cysticapnos vesicaria forma *brevilobus* Fedde: 287 (1924), syn. nov. Type: South Africa, [Western Cape], Stellenbosch and Swellendam, without date, Ecklon 21 (B, lecto.!, here designated).

Cysticapnos vesicaria forma *longilobus* Fedde: 287 (1924), syn. nov. Type: South Africa, [Western Cape], Brakdam, August 1897, R. Schlechter 11131 (B, lecto.!, here designated; MO, iso.!).

Cysticapnos vesicaria forma *latilobus* Fedde ms. (without collector or date, B).



FIGURE 8.—*Cysticapnos vesicaria* subsp. *vesicaria*: A, portion of flowering stem; B, base of plant; C, flower, lateral view; D, lower outer petal; E, inner petals; F, gynoecium, lateral view; G, detail of nectary; H, infructescence (nearside lower leaf segment omitted); I, half normal fruit; J, dwarf fruit; K, seed. Scale bar: A, B, H–J, 10 mm; C–G, 1 mm; K, 0.5 mm. Artist: John Manning.

Cysticapnos alexandrina Link & Otto, nom. nud.

Cysticapnos grandiflora E.Mey.: 95 (1844), nom. nud.

Cysticapnos grandiflora [Bernh.] sensu Lidén: 106 (1986), nom. nud. [cited as *C. grandiflora* Bernh. in *Linnaea* 12 (as '13') by Lidén: 664 (1986), but not mentioned therein].

Raceme 10–20(–45) mm long, 1–3(4)-flowered. Outer petals 7–9 mm long with wings 2–3 mm wide.

Distribution and ecology: widespread through the southwestern and southern Cape, from the northern Bokkeveld Plateau southwards along the west coast and the inland mountains of the southwestern Cape as far east as Still Bay on the coast and Outdshoorn in the Little Karoo (Figure 9). Plants are most commonly found in sandy soils in fynbos and thicket, especially along the coast, but inland populations occur on finer-grained clay or limestone soils in renosterveld.

The typical subspecies is characterized by short, 1–4-flowered racemes and relatively small flowers, 8–10 mm long, borne close to the stem and thus relatively inconspicuous.

3.3b. subsp. **namaquensis** J.C.Manning & Goldblatt, subsp. nov.

Cysticapnos parviflora Lidén: 106 (1986), syn. nov. Type: South Africa, Northern Cape, 3018 (Kamiesberg): Farm Kamagap, 10 km NE of Bitterfontein on Kliprand road, (–CC), 10 September 1974, *Nordenstam & Lundgren 1803* (S, holo.!).

Racemus (20–)30–40(–80) mm longus, 3–5(–7)-flora, alis petali externis 3–5 mm latis.

TYPE.—Northern Cape, 3018 (Kamiesberg): Langkloof, renosterveld near river, 735 m, (–CA), 7 September 2006, *Snijman 2081* (NBG, holo.; K, iso.).

Raceme (20–)30–40(–80) mm long, 3–5(–7)-flowered. Outer petals 9–13 mm long with wings 3–5 mm wide.

Distribution and ecology: widespread through the higher-lying parts of Namaqualand, from Nuwerus northwards into the Richtersveld, and into southern Namibia on the Numaisspitze at the southern edge of the Huib Hock Plateau (Figure 9). Plants grow in sandy or gritty soils, often along seasonal washes and watercourses.

This subspecies is distinguished from subsp. *vesicaria* by the mostly longer, more floriferous racemes bearing 3–7 flowers. Populations between Garies and Springbok have especially large flowers, 10–15 mm long, and constitute a particularly attractive form of the species in which the racemes of showy flowers project conspicuously above the stems that twine through the upper twigs of supporting shrubs. The collections from southern Namibia, in contrast, have the small flowers of subsp. *vesicaria* but their longer, more floriferous racemes are typical of subsp. *namaquensis*.

A cultivated plant grown in Europe in 1974 from seed collected between Bitterfontein and Kliprand produced unusually small flowers and a single dwarf fruit, and was described as the new species *Cysticapnos parviflora* by Lidén but is evidently nothing more than a poorly developed individual of this subspecies. The wild collection has the relatively many-flowered racemes and large flow-

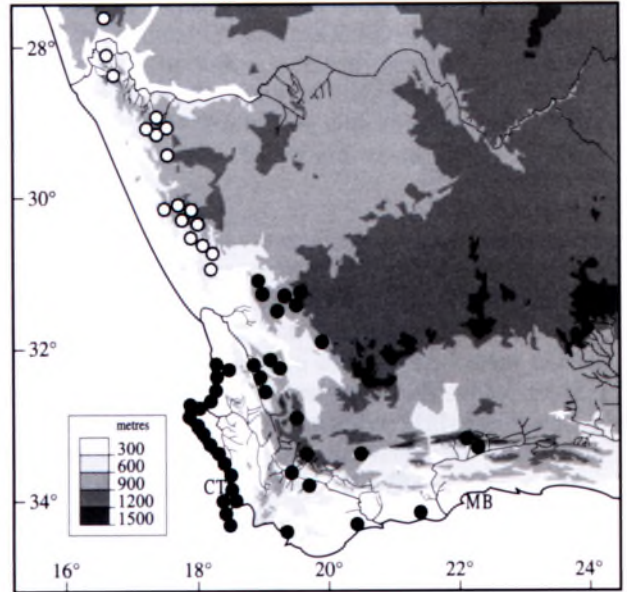


FIGURE 9.—Known distribution of *Cysticapnos vesicaria* subsp. *vesicaria*, ●; and *C. vesicaria* subsp. *namaquensis*, ○.

ers typical of subsp. *namaquensis* with the petal wings up to 7 mm wide, compared to 2 mm in the cultivated material (Lidén 1986). The seeds of these cultivated plants, which measured 0.8 mm in diameter, were contrasted against the larger seeds 1.3 mm in diameter of *C. grandiflora* (Lidén 1986) but seed size is variable in *C. vesicaria* and can range from 0.8–1.5 mm in diameter within a single collection (e.g. *Buys 474*, *Rosch 547*). This apparent difference in seed size is thus not significant. No further material matching the cultivated plants, from which much of the description and illustrations were based, has been collected despite the fact that the type locality is on a well-travelled road through Namaqualand.

History: although mostly quite distinct from the southern forms of the species in the wild, the larger-flowered northern populations have not been recognized taxonomically until now.

II. Subtribe **Fumariinae**

Scandent annuals (rarely perennial) with 2–4-pinnate leaves, lacking tendrils. *Racemes* pedunculate. *Flowers* white to pink, or yellow, upper petal spurred. *Style* deciduous; stigma with two papillae. *Fruit* a hard-walled nutlet, one-seeded, indehiscent, usually with two apical germination pores.

Four genera: *Cryptocapnos*, *Fumaria*, *Fumariola* and *Rupicapnos*. Mainly Mediterranean to central Asia, also North and East Africa, and the Himalayas.

4. **Fumaria** L., *Species plantarum*: 699 (1753). Type species: *Fumaria* L.

Brittle, semisucculent, glabrous, erect or diffuse annuals; stems quadrate, with obscure unicellular papillae along angles; sap watery, clear. *Leaves* alternate, 2–4-pinnately compound, primary divisions alternate or opposite; ultimate leaflets linear to obovate, without tendrils but sometimes petiolule and rachis prehensile. *Inflorescence* sessile or pedunculate, terminal but leaf-

opposed through rapid growth of axillary bud, racemose, pedicels often thickening in fruit; bracts scale-like, petaloid, irregularly toothed. *Flowers* zygomorphic, bilabiate, pink, unscented. *Sepals* 2, lateral, much shorter than petals, scale-like, petaloid, often irregularly toothed. *Petals* 4 in 2 series; outer petals larger, naviculate-spathulate, laterally winged apically, upper spurred at base, inner petals apically connate, clawed, limb inflated with dorsal crest, claw basally adnate to upper petal. *Stamens* 6, diadelphous in abaxial and adaxial bundles of 3; filaments of each bundle fused, lanceolate, membranous, clasping ovary, upper filament cluster adnate to margins of dorsal petal basally to form small chamber, with nectary decurrent on dorsal petal into spur. *Ovary* subglobose; ovules 1 or 2; style longer than ovary, ± slightly upcurved or flexed upwards apically, deciduous; stigma compressed, 2-lobed. *Fruit* ± erect or pendulous, subglobose or obreniform, smooth or rugulose, indehiscent and dropping entire, exocarp papery, endocarp hard and bony with paired apical germination pores. *Seed* solitary, lenticular, thin-walled, without elaiosome.

± 50 spp., Mediterranean to India and east tropical Africa, mainly North Africa and Spain.

Key to naturalized species

- 1a Peduncle longer than raceme; pedicels recurved, 3–5 mm long; sepals large, 4–6 mm long 4.1 *F. capreolata*
- 1b Peduncle shorter than raceme; pedicels stiffly suberect or spreading, sometimes recurving slightly in fruit, 1.5–2.5 mm; sepals small, 0.5–3.0 mm long:
 - 2a Leaves not as finely divided, parsley-like, ultimate segments oblanceolate-obovate (rarely ± linear); flowers pink and purple, 7–10 mm long, including spur; bracts 1.0–1.5 mm long, half to three-quarters as long as pedicels 4.2 *F. muralis*
 - 2b Leaves finely divided, almost dill-like, ultimate segments linear; flowers white turning pink, and purple, ± 5 mm long, including spur; bracts 2–3 mm long, as long as or longer than pedicels 4.3 *F. parviflora*

4.1. ***Fumaria capreolata* L.**, *Species plantarum*: 701 (1753); Sell: 256 (1964); Lidén: 67 (1986); Walsh & Norton: 407 (2007). Type: France, prope Olbyam Galliae Narbonense (*UPS-LINN74560*, holo.).

Sprawling or scandent, branching annual up to 1 m. *Leaves* bipinnately compound, rachis sometimes flexuous, ultimate segments obovate, dissected almost to base, lobes elliptical, apiculate-aristate. *Inflorescence* pedunculate, up to 80 mm long in fruit; raceme shorter than peduncle, 10–25(–35)-flowered; pedicels recurved, 3–5 mm long, apically thickened in fruit; bracts patent, not clasping pedicel, linear-lanceolate, 2.5–4.0 × 0.5–0.8 mm. *Flowers* creamy white or pale pink with dark reddish tips. *Sepals* peltate, ovate, 4–6 × 2.5–4.0 mm, irregularly toothed. *Petals*: outer petals naviculate, upper spathulate and apically short-winged, wings reflexed, ± 0.5 mm wide, spurred at base, spur compressed saccate, 2.5–3.5 mm long, lower linear with rudimentary apical wings, 8–9 × 1.0–1.5 mm; inner petals 7–9 mm long, claw ± 2 mm long, adnate to upper petal in lower 1 mm, blade inflated, narrowly oblong, 5–7 × 1 mm, with fleshy dorsal crest ± 0.5 mm wide. *Stamens*: filament bundles lanceolate-attenuate, 5–6 × 1 mm; anthers ± 0.25 mm long, yellow. *Ovary* subglobose, 1.5 mm diam., green; style slightly curved, 4–5 mm long, green, deciduous. *Fruit* globose, 2.0–2.5 mm diam., indehiscent and drop-

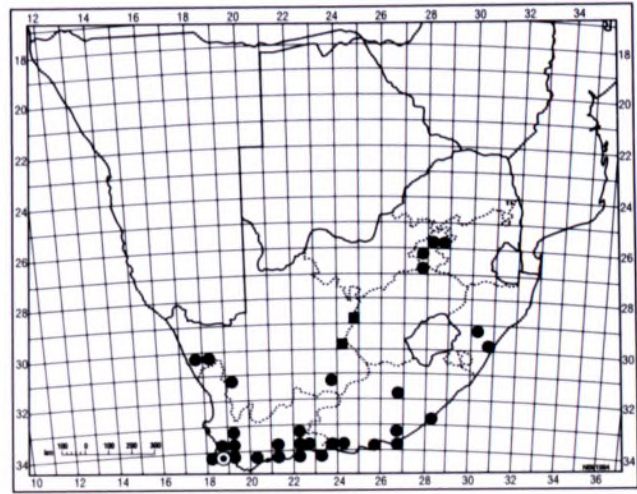


FIGURE 10.—Known distribution in southern Africa of *Fumaria capreolata* and *F. muralis*, ○, *F. muralis*, ●, and *F. parviflora*, ■.

ping entire, brown, exocarp membranous, finely tuberculate or almost smooth, endocarp woody with small hour-glass-shaped apical pit. *Seed* not seen. *Flowering time*: September to October.

Distribution and ecology: native to the Mediterranean and southwestern Europe but widely naturalized in warmer temperate countries, including southern Australia. Known in South Africa from a single collection made near Somerset West in Western Cape in 1952 (*Parker 4818*) (Figure 10), it is so far at most an occasional adventive here.

4.2. ***Fumaria muralis* Sond. ex W.D.J.Koch**, *Synopsis florae germanicae et helveticae*, edn 2, part 3: 1017 (1845); Sell: 257 (1964); Lidén: 78 (1986); Walsh & Norton 408 (2007). Lectotype designated by Walsh: 496 (1992): Germany, Hamburg *in muris*, July 1844, *Sonder s.n.* (*MEL1584466*, lecto.).

4.2a. subsp. ***muralis***

F. officinalis var. *grandiflora* DC.: 135 (1824). Type: South Africa, without precise locality or collector (G-BU, holo.).

F. officinalis var. *capensis* Harv.: 18 (1894), syn. nov. Type: South Africa, [Western Cape], Witzenberg, without date, *Ecklon & Zeyher 25* (TCD, holo.; PRE, SAM, iso.).

Sprawling or scandent, branching annual up to 0.5 m, with clear sap. *Leaves* bipinnately compound; rachis sometimes flexuous; ultimate segments obovate, dissected almost to base, lobes elliptical (rarely ± linear), apiculate-aristate, terminal segment rarely without a blade. *Inflorescence* pedunculate, up to 30 mm long in fruit, 3–12-flowered; pedicels suberect or spreading, 2.0–2.5 mm long, thickened, firm and sometimes slightly recurved in fruit; bracts erect, clasping pedicel, 1.0–1.5 × 0.5 mm, irregularly toothed. *Flowers* pale to deep pink with dark reddish tips. *Sepals* peltate, ovate, 2–3 × 1.5–2.0 mm, irregularly toothed. *Petals*: outer petals naviculate, 5–7 × 1.0–1.5 mm, upper petal spathulate and apically short-winged, wings reflexed, ± 0.5 mm wide, spurred at base, spur compressed saccate, 2.0–3.5 mm long, lower petal linear with rudimentary apical wings; inner petals 5–7 mm long, claw ± 1.5 mm long, adnate to upper petal in lower 1 mm, blade inflated, nar-

rowly oblong, 4–5 × 1 mm, with fleshy dorsal crest ± 0.5 mm wide. *Stamens*: filament bundles lanceolate-attenuate, 5–6 × 1 mm; anthers ± 0.25 mm long, yellow. *Ovary* subglobose, 1.5 mm diam., green; style ± straight or slightly curved, 4–5 mm long, green, deciduous. *Fruit* suberect, globose, 2.0–2.5 mm diam., indehiscent and dropping entire, brown, exocarp membranous, finely tuberculate or ± smooth, endocarp woody with small hourglass-shaped apical pit. *Seed* depressed-subglobose, 1.5–2.0 mm diam., testa membranous, containing scattered, elongate orange deposits. *Flowering time*: mainly August to October, later or earlier in gardens. Figure 11.

Distribution and ecology: native to Europe but introduced elsewhere, including Australia and New Zealand. The species is widely distributed in South Africa as a ruderal through the wetter, more temperate parts of both winter and summer rainfall regions (Figure 10). It is especially common in the southwestern and southern Cape but has also been recorded from the higher-lying Kamiesberg in central Namaqualand and into the Eastern Cape, in KwaZulu-Natal between Durban and Pietermaritzburg, and in Gauteng, with isolated collections from Kimberley, Bloemfontein and Phalaborwa. It is found along the margins of cultivated lands and in fallow fields, in waste places, and as a weed in gardens. *Fumaria muralis* is essentially cleistogamous, the anthers dehiscing before the petals separate, and the style abscising from the ovary by anthesis.

The species appears to have been first collected in South Africa during the latter part of the eighteenth century by Carl Thunberg, who observed (Thunberg 1823) that it had become widely established in the southwestern Cape, both in gardens and outside of them. This very early appearance of *Fumaria muralis* makes it one of the first exotic plant species to naturalize in South Africa. Other early collections from the southwestern Cape, made during the first half of the eighteenth century, include those by Christian Ecklon & Carl Zeyher (Ecklon & Zeyher 25) and by Johann Drège (PRE24456). Collections from the end of the century by Henry George Flanagan and Alice Pegler record its occurrence in the Eastern Cape, and it had reached central Namaqualand, KwaZulu-Natal and Gauteng by the early decades of the twentieth century.

It is almost certain that *Fumaria muralis* was an accidental introduction to South Africa, probably among wheat seed brought from Europe. Species of *Fumaria* are common weeds of cereal crops in Australia and wheat was already cultivated widely in the southwestern Cape by the time that *F. muralis* was first collected in the region by Thunberg (Thunberg 1823). This mode of introduction would also explain its rapid spread through the country. The alternative, that it was a deliberate introduction, is not supported by any evidence. The small flowers of *F. muralis* make it useless as an ornamental and although the closely allied *F. officinalis* is used medicinally in Europe (Launert 1981), the absence of any mention of the species in Pappe's early treatise on South African medicinal plants (Pappe 1868) (and which included other introductions) or in the later compendium by Watt & Breyer-Brandwijk (1932), suggests that it was not introduced for medicinal purposes.

Early collections of the species from southern Africa were identified as forms of *Fumaria officinalis* L. (at that time *F. muralis* had still to be described), and even until recently *F. muralis* was often treated as a synonym of *F. officinalis*. True *F. officinalis* is characterized by more pronouncedly spatulate lower petals, and nutlets that are broader than long, apically truncate or emarginate and often obreniform in shape (Sell 1964; Lidén 1986). When pressed, green fruits of *F. muralis* may split open at the apex and thus appear to be obreniform, and this has resulted in some collections being misidentified as *F. officinalis*. Although an uncommon introduction in Australia, *F. officinalis* does not yet appear to have been recorded in South Africa.

Nomenclatural note: Harvey (1894) treated the South African material as *Fumaria officinalis* var. *capensis* Harv., based on Ecklon & Zeyher 25, and although his citation of the earlier name *F. capreolata* β. *burchellii* DC. (1824) would render his name superfluous were de Candolle's epithet to be accepted at varietal level, we interpret de Candolle's hesitant citation of the rank of his name as *F. capreolata* β? *burchellii* to be sufficient grounds for considering the name rankless and thus without priority at varietal rank (McNeil *et al.* 2006: Art. 52.1).

4.3. *Fumaria parviflora* Lam., Encyclopédie méthodique. Botanique 2: 567 (1788); Sell: 258 (1964); Lidén: 88 (1986); Walsh & Norton: 410 (2007). Type: In cult. Paris, of Mediterranean origin, Lamarck (P-LAM, holo.).

4.3a. var. *parviflora*

Sprawling, branching annual up to 0.5 m. *Leaves* ternately compound; primary divisions alternate or opposite, ultimate segments finely dissected to base, lobes linear, apiculate-aristate. *Inflorescence* up to 30 mm long in fruit, (7–)10–15(–22)-flowered; pedicels suberect, 1.5–2.0 mm long, thickened and firm in fruit; bracts erect, clasping pedicel, 2.0–3.0 × 0.5 mm, irregularly toothed. *Flowers* white, turning pink with age, with dark reddish tips. *Sepals* cordate, broadly ovate, 0.5–1.0 × 0.5–0.7 mm, irregularly toothed. *Petals*: outer petals naviculate, 3–4 × ± 1 mm, upper petal spatulate and apically short-winged, wings patent, ± 0.5 mm wide, spurred at base, spur compressed saccate, 1.0–1.5 mm long, lower petal linear with rudimentary apical wings; inner petals 3–4 mm long, claw ± 1.5 mm long, adnate to upper petal in lower 1 mm, blade inflated, narrowly oblong, ± 2.5 × 1 mm, with fleshy dorsal crest ± 0.5 mm wide. *Stamens*: filament bundles lanceolate-attenuate, 2.5–3.0 × 1 mm; anthers ± 0.1 mm long, yellow. *Ovary* subglobose, ± 1 mm diam., green; style flexed sharply upwards apically, ± 2 mm long, green, deciduous; ovule 1, lateral. *Fruit* suberect, globose, ± 2 mm diam, indehiscent and dropping entire, brown, exocarp membranous, finely rugose-tuberculate, endocarp woody with small hourglass-shaped apical pit at styler end. *Seed* not seen. *Flowering time*: August to February.

Distribution and ecology: native to the Mediterranean but widely naturalized elsewhere, including Australia, where it is scattered but uncommon. In South Africa the species appears to be naturalized only in the drier western parts of the Northern Cape and Free State, where it has been recorded from Hopetown and Kimberley (Fig-

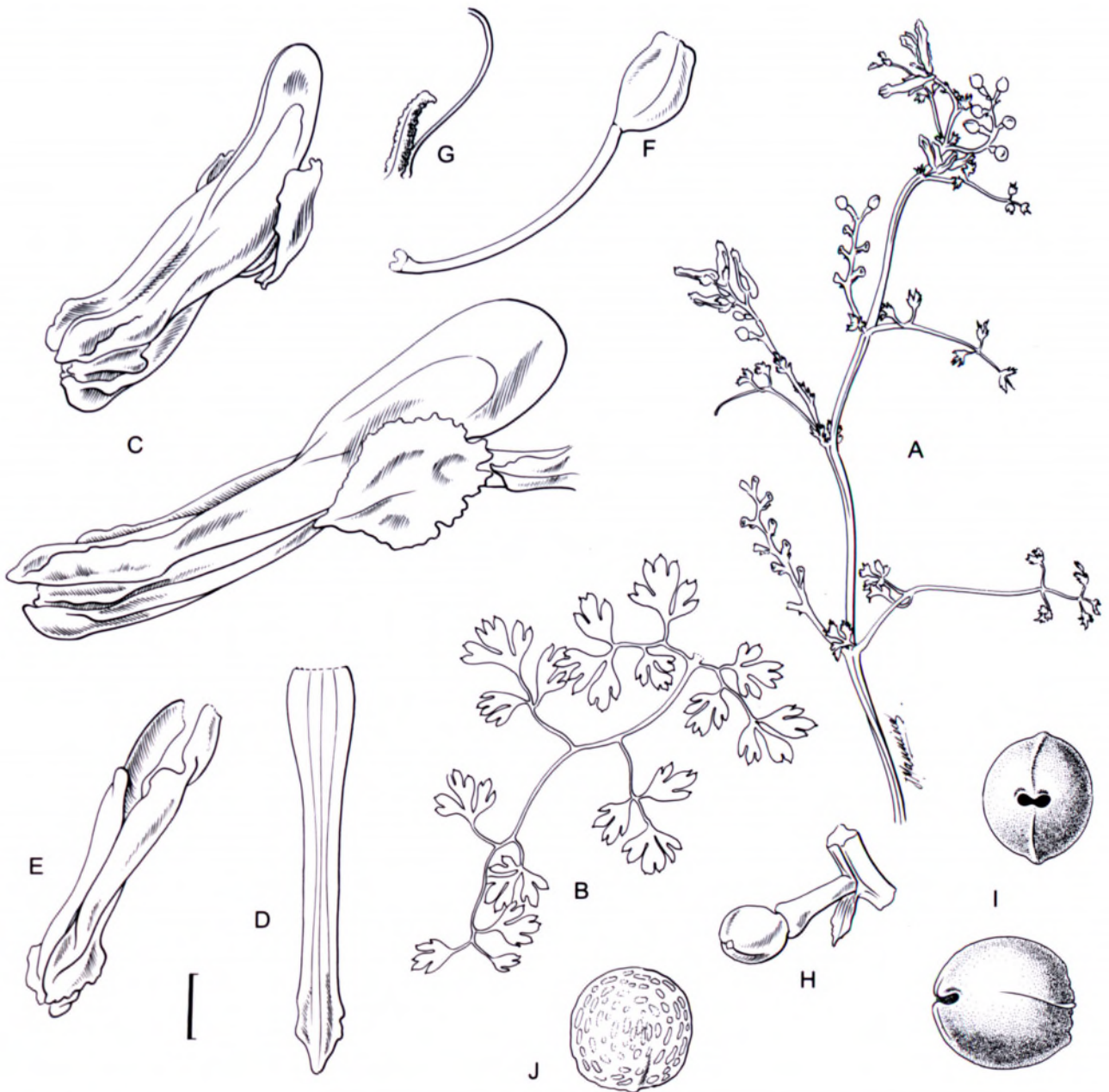


FIGURE 11.—*Fumaria muralis*: A, portion of stem; B, detached lower leaf; C, flower, three-quarter and lateral views; D, lower outer petal; E, inner petals; F, gynoecium, lateral view; G, detail of nectary; H, fruit; I, endocarp, front and dorsal views; J, seed. Scale bar: A, B, 10 mm; C–J, 1 mm. Artist: John Manning.

ure 10), typically along irrigation ditches or channels, where it is regarded as a troublesome weed, forming dense stands in wet places and choking the canals. The species is evidently a recent introduction to the country, and no records from earlier than the latter decades of the twentieth century have been seen.

Fumaria parviflora, like *F. muralis*, is essentially cleistogamous, the anthers dehiscing before the petals separate, and the style abscising from the ovary by anthesis.

OTHER SPECIMENS EXAMINED

The taxa are indicated in brackets by the number assigned to them in the text, followed by the herbarium acronym.

Abbot 4775, 5509 (3.2) MO, NH. Acocks 10477 (4.2) PRE; 14883, 16960, 17782 (2) PRE; 14950 (3.3b) PRE; 20433 (3.2) PRE; 20653, 21571, 22723 (3.1) PRE. Adamson 1936 (3.3a) BOL; 2103 (1a) BOL. Andreae 390 (3.3a) NBG. Axelson 477 (3.3a) NBG.

Baker 6 (4.2) PRE. Balkwill, Manning & Cadman 1145 (3.2) MO, NU, PRE. Barker 1360 (3.3b) NBG; 5929 (3.3a) NBG. Baur ex Marloth 11457 (3.1) PRE. Bayer 227 (3.1) NBG; 240 (4.2) NBG. Bayliss 87 (3.2) MO. Behr 481 (4.2) PRE. Bester 2700 (3.2) NH; 3953 (3.2) PRE. Bohnen 4762 (4.2) NBG, PRE. Bolus 1003 (3.1) BOL; 4697 (1a) BOL, NBG; 2702, 8052, 12596 (3.3a) BOL; 8920 (2) PRE. Bond 509 (3.3a) NBG. Booi 132, 135 (4.2) PRE. Borchardt PRE463 (3.1) PRE. Bosenberg & Rutherford 75 (3.3a) NBG. Botes 397 (3.1) NBG. Boucher 528 (3.1) NBG, PRE; 6579 (3.3a) NBG. Braun 2224 (3.2) PRE. Bremer 281 (3.3a) PRE. Brooke 3 (3.3a) BOL. Brynard 255 (4.2) PRE. Burgers 2114 (4.2) NBG; 2933 (3.3a) NBG. Burrows 6393 (3.2) PRE. Burt-Davy 10811 (4.2) PRE. Buys 474 (3.3a) NBG.

Cairns PRE54105 (4.2) NBG, PRE. Castelnau PRE24458 (4.2) P, PRE. Cloete & Haselau 283 (2) NBG; 285 (3.3a) NBG. Coleman 312 (3.2) PRE. Compton 2688, 24323 (2) NBG; 3508 (3.1) BOL; 6808,

17216 (3.3b) NBG; 21516 (3.2) NBG, PRE; 22296 (1a) NBG. *Crosby 660* (3.3b) PRE. *Cruz 54* (3.3b) NBG; 126 (4.2) NBG.

Dahlstrand 2112 (3.3a) MO, NBG, PRE; 2453 (4.2) PRE. *De la Bat s.n.* (3.1) NBG. *De Vos 1461* (3.1) NBG. *Devenish 513, 1203* (3.2) PRE. *Dieterlen 873* (3.2) PRE, SAM. *Dobay 65* (3.1) NBG; 66 (3.3a) NBG. *Dive 104* (3.2) PRE. *Drège 3847* (3.1) BOL; *PRE24456* (4.2) P, PRE.

Ecklon 25 (4.2) PRE. *Eliovson 35* (3.3b) PRE. *Esterhuysen 231, 11226* (1a) PRE; 564, 11227 (3.1) PRE; 5539 (2) BOL; 5825 (3.1) NBG; 11848 (1a) BOL, PRE. *Evrard 8934* (3.3b) PRE.

Fabian 1244 (3.2) PRE. *Fellingham 236* (4.2) NBG, PRE. *Flanagan 806* (4.2) PRE, SAM. *Fourcade 398* (4.2) NBG; 506 (3.1) BOL, MO; 904 (1b) BOL. *Fugler 101* (4.2) NBG, PRE.

Galpin 1803 (3.2) BOL; 6569 (3.2) BOL, NH, SAM; 8229 (4.2) PRE. *Giess 13070* (3.3b) PRE. *Giffen 710* (4.2) PRE. *Gill 64* (4.2) PRE. *Gillett 547, 1080* (3.1) NBG; 3380 (1a) NBG, PRE. *Glass 21* (4.2) NBG. *Goldblatt 1980* (3.1) MO; 2334 (3.3a) MO, PRE; 5793 (2) PRE. *Goldblatt & Manning 10520, 10554* (2) NBG; 10577 (2) BOL, MO, PRE; 13016 (3.1) MO, NBG, PRE. *Goldblatt & Porter 12396* (3.3a) NBG; 12421 (2) MO, NBG. *Greene 1091* (3.2) NH. *Grobler 38* (3.3b) PRE. *Gubb KMG11151* (4.3) PRE. *Guillarmod 597, 1079* (3.2) PRE. *Guthrie 2538* (3.1) NBG.

Hahndiek 15 (3.3a) NBG. *Hall 4464* (2) NBG, PRE; *s.n.* (3.3b) NBG. *Hanekom 688* (4.2) NBG, PRE; 1189 (3.3a) NBG, PRE. *Harris 30* (4.2) PRE. *Harvey s.n.* (1a) PRE, TCD. *Haynes 1110* (1a) NBG, PRE; 1110A (3.1) PRE. *Heinecken 103* (4.2) PRE. *Helme 2615* (3.2) NBG. *Herre s.n.* (3.3b) NBG. *Heyns s.n.* (3.3a) NBG. *Hilliard & Burt 6670* (3.2) MO, NU; 8869, 12192 (3.2) NU; 13025 (3.3a) NU, PRE; 14968 (3.2) NU, PRE. *Hilton-Taylor 1185* (3.3b) NBG. *Hugo 442* (3.3a) NBG; 542, 2432, 2959 (3.3a) NBG, PRE. *Hutchinson 263* (3.3a) BOL, PRE; 780 (2) K, PRE.

Jacobsz 2013 (3.2) NBG.

Kemper IPC621 (3.1) NBG. *Killick 2277, 4390* (3.2) PRE. *Kinges 1761* (4.2) PRE. *Kok & Pienaar 1214* (4.2) PRE. *Kroon 38* (4.2) PRE. *Kruger 513* (4.2) NBG, PRE.

Le Roux 2426 (3.3a) PRE; 2483 (3.3a) NBG, PRE; *Le Roux & Ramsey 365* (3.3a) NBG, PRE. *Leipoldt 20752* (2) BOL. *Levy 3217, 11320* (3.3a) BOL; 3453, 8511 (1.1a) BOL; 4065 (3.3b) BOL; 50572 (3.3a) BOL, PRE. *Lewis 1905, 1906* (3.3b) SAM; 19829 (3.1) BOL. *Linder 2196* (3.3a) BOL. *Loubser 3457* (3.1) NBG. *Low 925* (4.2) NBG, PRE; 976 (4.2) NBG; 927a (3.3a) NBG, PRE; 2799 (3.3a) NBG.

MacOwan 1247 (3.1) BOL; 1713 (3.2) SAM; *SAM14025* (3.1) SAM. *Maguire 288* (3.3b) NBG; 1887 (2) NBG; 1916 (3.3a) NBG. *Manning 3017* (4.2) NBG. *Manning, Hilliard & Burt 16020* (3.2) E, NU. *Marais 1352* (3.2) BOL, PRE. *Marloth 237* (3.3a) PRE; 570 (4.2) PRE; 3612 (1a) PRE; 6773 (3.3b) NBG, PRE; 12448 (3.3b) PRE. *Marsh 370* (3.3a) NBG, PRE; 399 (3.1) NBG, PRE. *Matthews 901* (3.2) NBG. *Mauve 2861* (4.2) PRE; 4544 (3.3a) PRE. *Medley-Wood 4597, 5237* (3.2) NH. *Meyer 3735* (4.2) PRE. *Moffet 71* (4.2) NBG, PRE; 191 (3.3a) NBG, PRE. *Mogg 1055, 11688* (4.2) PRE. *Montgomery 48* (3.1) NBG. *Moriarty 723* (3.3a) NBG. *Muir 5* (3.3a) PRE; 6 (4.2) PRE; 2921 (3.1) PRE.

Nelson 11622 (4.2) PRE. *Newnham Brothers PRE54096* (4.2) PRE. *Nicolson 2102* (4.2) PRE.

O'Callaghan, Fellingham & Van Wyk 2 (4.2) NBG, PRE. *Oliver 3716* (4.2) NBG, PRE; 4350 (4.2) NBG. *Oliver, Tölken & Venter 475, 643* (3.3b) NBG, PRE; *Olivier 90* (3.3a) NBG, PRE; 781 (4.2) NBG.

Parker 4235 (4.2) NBG; 4818 (4.1) NBG. *Pearson 172, 6603* (4.2) NBG. *Pegler 519* (4.2) PRE. *Perry & Snijman 2289* (3.3a) NBG, PRE; 2290 (2) NBG. *Phillips 1390* (4.2) SAM; 7616 (3.1) SAM; *s.n.* (3.3a) NBG. *Phillipson 717, 1449* (3.2) PRE; 717 (3.2) MO. *Phillipson & Hutchings 167* (3.2) K, MO, PRE. *Pienaar 1155, 1166* (3.3b) PRE. *Pillans 2859, 6921* (3.1) BOL. *Potts 5133* (3.2) BOL, PRE; 2817 (4.2) PRE. *Pretorius 270* (2) NBG. *Purcell SAM89465* (4.2) SAM.

Rennie s.n. (3.2) NU. *Roberts 3439* (3.2) PRE. *Retief 651* (4.2) PRE. *Rodin 1475* (3.3b) MO, PRE. *Rogers 3484* (3.1) MO. *Rösch 547* (3.3a) NBG; 644 (2) NBG. *Rösch & le Roux 696* (3.3b) PRE; 1452 (4.2) PRE. *Rourke 577* (3.3a) MO, NBG; 1114 (3.3a) MO, NBG, PRE. *Roux Grootfontein 132* (4.3) PRE. *Rubin 420* (4.2) PRE.

Schelpel 239 (3.3b) BOL; 506 (3.2) NU, PRE; 1443 (3.2) NU. *Schlechter 4596* (3.1) PRE; 4941 (3.3a) NBG, PRE; 10863 (2) MO; 10869 (2) BOL, PRE; 11060 (3.3b) BOL, MO; 11131 (3.3b) PRE. *Schmidt 383*

(3.3a) PRE. *Schmitz 8352* (4.2) PRE; 9312 (3.2) PRE. *Schönland 3636* (4.2) PRE. *Schweickerdt 2569* (3.3b) PRE. *Shearing 1295* (4.2) PRE. *Sidey 2242* (3.1) MO. *Sikhakhane & Williams 390* (3.2) NH, PRE. *Smith 3027* (3.3a) PRE. *Smuts s.n. PRE59122* (3.3a) PRE. *Staples 217* (3.2) PRE. *Steiner 529* (3.2) MO, NBG; 748 (2) NBG; 768 (3.3a) NBG; 861 (3.2) NBG; 921, 3657 (3.3b) NBG. *Stewart 1903* (3.2) MO, NU. *Steyn 14, 95* (4.2) PRE; 572 (3.3a) NBG; 592 (2) PRE. *Strey 2823* (3.3a) PRE; 11013, 3909 (4.2) PRE. *Stokoe SAM67430* (3.3a) SAM. *Strid & Strid 37430, 38077* (3.3a) PRE. *Symons 14553* (3.2) PRE.

Taylor 1553 (3.1) SAM; 2718 (3.3a) NBG; 3951, 8150 (4.2) NBG; 4103, 11827 (3.1) NBG; 4104, 7411 (3.3a) NBG, PRE; 7410, 7421 (3.1) NBG, PRE; 11788 (2) NBG, PRE; 11801 (3.3a) MO, NBG, PRE. *Theron 1089* (4.2) PRE. *Thode 5441, 5442, 6132* (3.1) NBG; 6133, 6134 (1.1a) NBG; 8267 (3.2) NBG; 9281 (3.3a) NBG; A473, A1140 (3.2) PRE; *s.n./A738* (1.1b) BOL, NH, PRE; A1878 (3.1) PRE; A1958 (3.3a) NBG, PRE; A1959 (4.2) NBG, PRE; STE5670 (3.2) NH. *Thompson 394, 1034* (3.3b) NBG, PRE; 1875 (3.1) NBG. *Thompson & Le Roux 49* (3.3b) MO, NBG, PRE. *Thorne SAM48867* (3.3b) SAM. *Trausel 365* (3.2) NU. *Tyson 498, 1728* (3.2) SAM; 640 (3.3a) NBG, PRE, SAM.

Van Breda 43, 80 (3.3a) PRE. *Van der Merwe 866* (4.2) PRE; 1746 (3.3a) NBG; 2557 (3.3a) PRE. *Van der Walt 157* (3.3b) NBG, PRE; *s.n.* (3.3a) NBG. *Van Jaarveld 1389* (3.3b) PRE. *Van Niekerk 814* (3.1) BOL. *Van Rooyen 2254* (3.3a) PRE. *Van Wyk 717* (4.2) NBG, PRE; 1244 (3.3a) NBG, PRE; 1937 (3.1) NBG, PRE; 1937A (3.3a) NBG; 6305 (3.3b) PRE. *Van Wyk & Abbott 12058* (3.2) PRE. *Van Wyk, Winter & Tilney 3458* (3.1) PRE. *Van Zyl 3122* (3.3a) NBG, PRE. *Venter 9537* (3.3b) PRE. *Verdoorn s.n. PRE54147* (3.1) PRE. *Victor 211* (4.2) PRE. *Viviers 602* (3.3a) NBG, PRE.

Walgate 295 (3.3a) NBG. *Walters 2004* (4.2) NBG. *Ward 606* (4.2) PRE. *West 630* (3.2) PRE. *Wiese 6* (4.2) NBG. *Williams 3320* (4.2) NBG. *Williamson 3562, 3916* (3.3b) NBG. *Wilman 1475* (3.3b) BOL. *Winkler 92* (4.2) NBG. *Wolley Dod* (3.1) BOL; 114 (1.1a) BOL. *Wright 1798* (3.2) NU.

Zantovska 117 (4.2) PRE. *Zeitsman & Zeitsman 1003* (3.3b) PRE; 1101 (2) PRE?; 1458 (3.2) PRE. *Zeyher 4936* (3.1) BOL, SAM; *PRE54116* (4.2) PRE; *SAM14029* (3.3a) SAM. *Zeyher, Preiss & Krauss SAM14028* (3.3a) SAM.

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REFERENCES

- ANGIOSPERM PHYLOGENY GROUP (APG). 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* 141: 399–436.
- BERNHARDI, J.J. 1838. Nachträgliche Bemerkungen über Papaveraceen und Fumariaceen. *Linnaea* 12: 651–668.
- BREMER, K., BREMER, B. & THULIN, M. 2003. Introduction to phylogeny and systematics of flowering plants. *Symbolae Botanicae Upsalienses* 33: 2. Department of Systematic Botany, Uppsala.
- BRUMMITT, R.K. & POWELL, C.E. 1992. *Authors of plant names*. Royal Botanic Gardens, Kew.
- BURCHELL, W.J. 1822. *Travels in the interior of southern Africa*. 2 vols. MacLehose, Glasgow. Reprinted 1953 by Batchworth Press, London.
- CHAMISSO, L.A. VON & SCHECHTENDAL, D.F.L. 1826. *Fumariaceae*. *Linnaea* 1: 556–570.
- DE CANDOLLE, A.-P. 1824. *Fumariaceae*. *Prodromus systematis regni vegetabilis* 1: 125–130. Treutel & Würtz, Paris.
- DON, G. 1831. *A general system of gardening and botany*, vol. 1. Rivington, London.
- FEDDE, F.K.G. 1924. *Cysticapnos vesicarius* (L.) heterokarp. *Repertorium specierum novarum regni vegetabilis* 19: 285–288.
- FOREST, F. & MANNING, J.C. in prep. A molecular phylogeny of the southern African Fumariaceae.

- FUKUHARA, T. 1995. Vascular pattern in the fruit of *Trigonocapnos* and *Discocapnos* (Papaveraceae–Fumarioideae). *International Journal of Plant Science* 156: 547–554.
- FUKUHARA, T. & LIDÉN, M. 1995a. Seed-coat anatomy in Fumariaceae–Fumarioideae. *Botanical Journal of the Linnean Society* 119: 323–365.
- FUKUHARA, T. & LIDÉN, M. 1995b. Pericarp anatomy in Fumariaceae–Fumarioideae. *Botanische Jahrbücher* 117: 499–530.
- GAERTNER, J. 1791. *De fructibus et seminibus plantarum*, vol. 2. Schramm, Tübingen.
- GOLDBLATT, P. & J.C. MANNING. 2000. Cape plants. A conspectus of the Cape flora of South Africa. *Strelitzia* 9. National Botanical Institute, Cape Town & Missouri Botanical Garden, St Louis.
- GUNN, M. & CODD, L.E. 1981. *Botanical exploration of southern Africa*. Balkema, Cape Town.
- HARVEY, W.H. 1894. Fumariaceae. In W.H. Harvey & O.W. Sonder, *Flora capensis* 1: 15–19. Reeve, Kent.
- HOLMGREN, P.K., HOLMGREN, N.H. & BARTLETT, L.C. 1990. *Index herbariorum*, edn 8. *Regnum vegetabile* 120. New York Botanical Gardens, Bronx, New York.
- HUTCHINSON, J. 1921. The genera of Fumariaceae and their distribution. *Bulletin of Miscellaneous Information, Royal Botanic Gardens, Kew* 1921: 97–115.
- KOCH, W.D. 1845. *Synopsis florum germanicae et helveticae*, edn 2, part 3. Gebhardt & Resiland, Leipzig.
- LAMARCK, J.B.A.P.M. DE. 1788. *Encyclopédie méthodique. Botanique* 2. Panckoucke, Paris.
- LAUNERT, E. 1981. *Edible and medicinal plants of Britain and northern Europe*. Hamlyn, London.
- LIDÉN, M. 1986. Synopsis of Fumarioideae (Papaveraceae) with a monograph of the tribe Fumariaceae. *Opera Botanica* 88: 1–133.
- LIDÉN, M. 1993. Fumariaceae. In K. Kubitzki, J.G. Rohwer & V. Bittrich, *The families and genera of vascular plants*, vol. II. Flowering plants–dicotyledons: 310–318. Springer, Berlin.
- LINNAEUS, C. 1753. *Species plantarum*. Salvius, Stockholm.
- LUCAS, G.L. 1962. Fumariaceae. In C.E. Hubbard & E. Milne-Redhead, *Flora of tropical East Africa*. Crown Agents for Oversea Governments and Administrations, London.
- McNEILL, J., BARRIE, F.R., BURDET, H.M., DEMOULIN, V., HAWKSWORTH, D.L., MARHOLD, K., NICOLSON, D.H., PRADO, J., SILVA, P.C., SKOG, J.E., WIERSMA, J.H. & TURLAND, N.J. 2006. International Code of Botanical Nomenclature (Vienna Code) adopted by the 17th International Botanical Congress, Vienna, Austria, July 2005. *Regnum vegetabile* 146. Koeltz Scientific Books, Königstein.
- MEYER, E. 1844. In J.F. Drège, *Zwei pflanzengeographische Dokumente*. Leipzig.
- MILLER, P. 1754. *Cysticapnos. The gardener's dictionary*, abridgement 4, vol. 3. Rivington, London.
- MOENCH, C. 1794. *Methodus*. Facsimile edn. Koenigstein-Taunus.
- PAPPE, L. 1868. *Flora capensis medicae*. Brittain, Cape Town.
- PERSOON, C.H. 1806. *Synopsis plantarum*, vol. 2. Cramerum, Paris.
- PRANTL, K. & KÜNDIG, J. 1889. Papaveraceae. In A. Engler & K. Prantl, *Die natürlichen Pflanzenfamilien*, vol. 3: 130–144. Engelmann, Leipzig.
- PRANTL, K. & KÜNDIG, J. 1891. Papaveraceae. In A. Engler & K. Prantl, *Die natürlichen Pflanzenfamilien*, vol. 3: 145. Engelmann, Leipzig.
- SCHLECHTER, R. 1899. *Plantae schlechterianae novae vel minus cognitae describuntur II*. *Botanische Jahrbücher* 27: 86–220.
- SELL, P.D. 1964. *Fumaria* L. In T.G. Tutin, V.H. Heywood, N.A. Burgess, D.H. Valentine, S.M. Walters & D.A. Webb, *Flora europaea*, vol. 1: 255–258. Cambridge University Press.
- THUNBERG, C.P. 1823. *Flora capensis*. Cottae, Stuttgart.
- WALSH, N.G. 1992. Lectotypification of *Fumaria muralis* Sond. ex Koch (Fumariaceae). *Muelleria* 7: 495, 496.
- WALSH, N.G. & NORTON, W. 2007. *Fumaria*. *Flora of Australia* 2: 405–412.
- WATT, J.M. & BREYER-BRANDWIJK, M.B. 1933. *The medicinal and poisonous plants of southern Africa*. Livingstone, Edinburgh.