

A revision of the genus *Choritaenia* (Apiaceae)

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Abstract

The poorly known monotypic genus *Choritaenia* (Apiaceae) is revised. *Choritaenia capensis* is a small annual herb endemic to the central parts of South Africa and has several peculiar morphological and carpological features not found in other genera of Apiaceae. The dorsally compressed, hairy fruits have “inter-rib” wings, and a woody endocarp with globose oil vesicles (rather than vittae or rib oil ducts) at regular intervals in the wings. The very short carpophore is hygrosopic and appears to be an adaptation for dispersal of the mericarps after rain. The phylogenetic position of *Choritaenia* within the family Apiaceae remains unclear, but it is presumed to be related to the subfamily Azorelloideae, the only group where some members have dorsally compressed fruits with woody endocarps.

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1. Introduction

Out of a total of 38 genera of Apiaceae indigenous to southern Africa (Burt, 1991), the genus *Choritaenia* Benth. is one of 19 endemics. Although small in number, these genera are very important for systematic studies because they have unusual morphological characters that are critical for understanding higher order relationships in the family as a whole. Molecular studies (Downie and Katz-Downie, 1999; Downie et al., 2001; Plunkett, 2001; Plunkett et al., 1996, 1997, 2004) showed that many South African genera are basally diverging in the family. These include not only predominantly woody groups such as *Polemanniopsis* B.L. Burt and *Steganotaenia* Hochst. (both close to Saniculoideae) and the new tribe Heteromorphae M.F. Watson and S.R. Downie (which includes *Anginon* Raf., *Dra-cosciadium* Hillard and B.L. Burt, *Glia* Sond., *Heteromorpha* Cham. and Schltdl. and *Polemannia* Eckl. and Zeyh.) but also perennial herbs such as the anomalous *Annesorhiza* Raf. and

Chamarea Eckl. and Zeyh. Another example is the monotypic *Choritaenia*, an annual herb of uncertain affinity with numerous unusual morphological characters.

Choritaenia has been traditionally placed in the hydrocotyloid tribe Mulinaceae DC. (Drude, 1898; Pimenov and Leonov, 1993) which was recently elevated to the rank of subfamily as Azorelloideae (Plunkett et al., 2004), but it lacks the characteristic lateral wings of most genera in this tribe (Liu, 2004). Furthermore, it has oil cells (oil vesicles) rather than rib ducts or vittae (Sonder and Harvey, 1862; Bentham, 1867, 1877; Phillips, 1951; Hiroe, 1979; Burt, 1991; Van Wyk, 2000). The purpose of this paper is to revise the genus and to provide, for the first time, detailed and accurate morphological and carpological information as a basis for future phylogenetic studies.

2. Materials and methods

Leaves, bracts, bracteoles, flowers and mature fruits from different specimens of *Choritaenia capensis* were rehydrated for illustrations and photographs. The voucher specimens are Acocks 713, Brueckner 945, Orpen 34 and Smith 540, all from the South African National Herbarium in Pretoria (PRE). Two rehydrated mature fruits (from Smith 540) were placed in FAA for a minimum of 24 h and then embedded in glycol methacrylate (GMA) following the procedure of Feder and

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O'Brien (1968). The method was modified to a minimum of 24 h for the first two infiltrations and a minimum of five days for the third infiltration. Transverse sections, about 5 μm thick, were cut using a Porter-Blüm ultramicrotome. Samples were stained using the periodic acid-Schiff/toluidine blue staining method (Feder and O'Brien, 1968) and photographed. Terminology is illustrated in Fig. 3. Additional fruit samples were rehydrated and the exocarps removed in order to study (and photograph) the unusual secretory structures in three dimensions.

3. Results

3.1. Vegetative morphology

The plant is a compact, prostrate, annual herb up to 35 cm in diameter but often much smaller (Fig. 1). Stems are very thin, 0.5–1.5 mm diameter, glabrous and slightly ribbed. The leaves are glabrous and have long petioles that are somewhat sheathing at their bases (Fig. 2a1–3). A distinctive feature is the irregularly to subternately dissected lamina that terminates in narrowly oblong ultimate segments.



Fig. 1. *Choritaenia capensis* showing compact, prostrate habit and abundance of fruits.

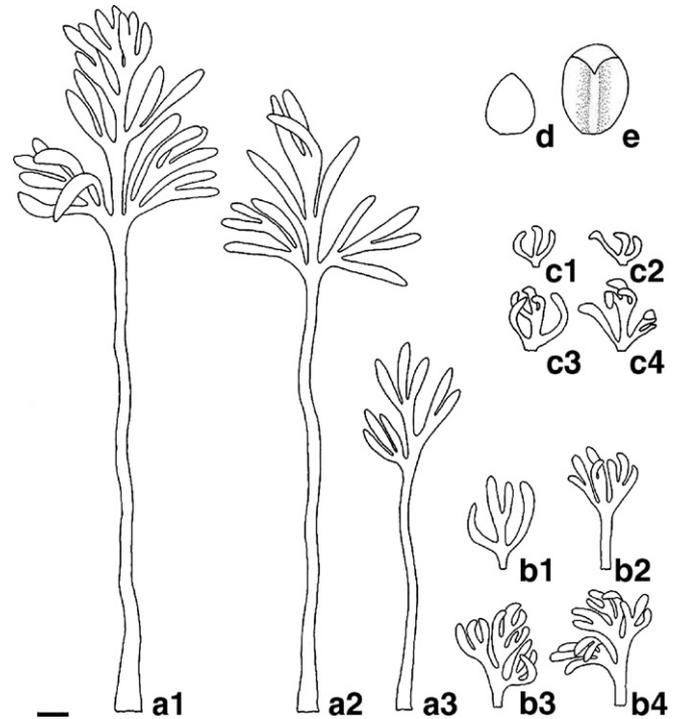


Fig. 2. Basal leaves (a1–a3), bracts (b1–b4), bracteoles (c1–c4), sepal (d) and petal (e) of *Choritaenia capensis*: The variation in leaves, bracts and bracteoles on a single plant is shown (all from Smith 540, PRE). Scale bar=1 mm in a–c and 0.18 mm in d and e.

3.2. Reproductive morphology

Terminal and lateral umbels are borne in large numbers along the slender stems (Fig. 1). The foliaceous bracts (Fig. 2b1–4) and bracteoles (Fig. 2c1–4) are dissected and resemble the leaves. The flowers are white or may turn purplish with age, with both the calyx (Fig. 2d) and petals (Fig. 2e) glabrous. The calyx lobes are short and ovate. The petals are ovate, with a short, inflexed apex, a distinct keel along the dorsal surface and a corresponding groove on the inner surface. The ovary is villous and the disc is broad and slightly raised, with a somewhat undulate margin (Fig. 3a). Styles are short and linear, without conspicuous stigmas. The stamens are as long as the petals.

The fruit is orbicular in dorsal view (Fig. 3b–d) and somewhat biconvex due to the convex outer surfaces (Fig. 3g), crowned with a persistent disc and styles, and covered with long, unicellular, stiff hairs (Fig. 3b–d, h). Hairs on the dorsal sides are short and club-shaped (slightly broader towards the apices). The edges of the mericarps, however, are remarkably different in vestiture, bearing long, thin hairs. The mericarps do not separate, except when soaked or rehydrated (Fig. 3e, f). They are convex on the outer surfaces and flat on the inner surfaces. Two “inter-rib” marginal wings are present, i.e. each wing is situated between the lateral and marginal vascular bundles (shown as small dots in Fig. 3h and labelled “lvb” and “mavb” respectively). Each mericarp has seven vascular bundles and not five as in almost all other Apiaceae. Five of these are located on the dorsal side of the mericarp and two on the commissural side (Fig. 3c, d). Rib ducts are absent and there

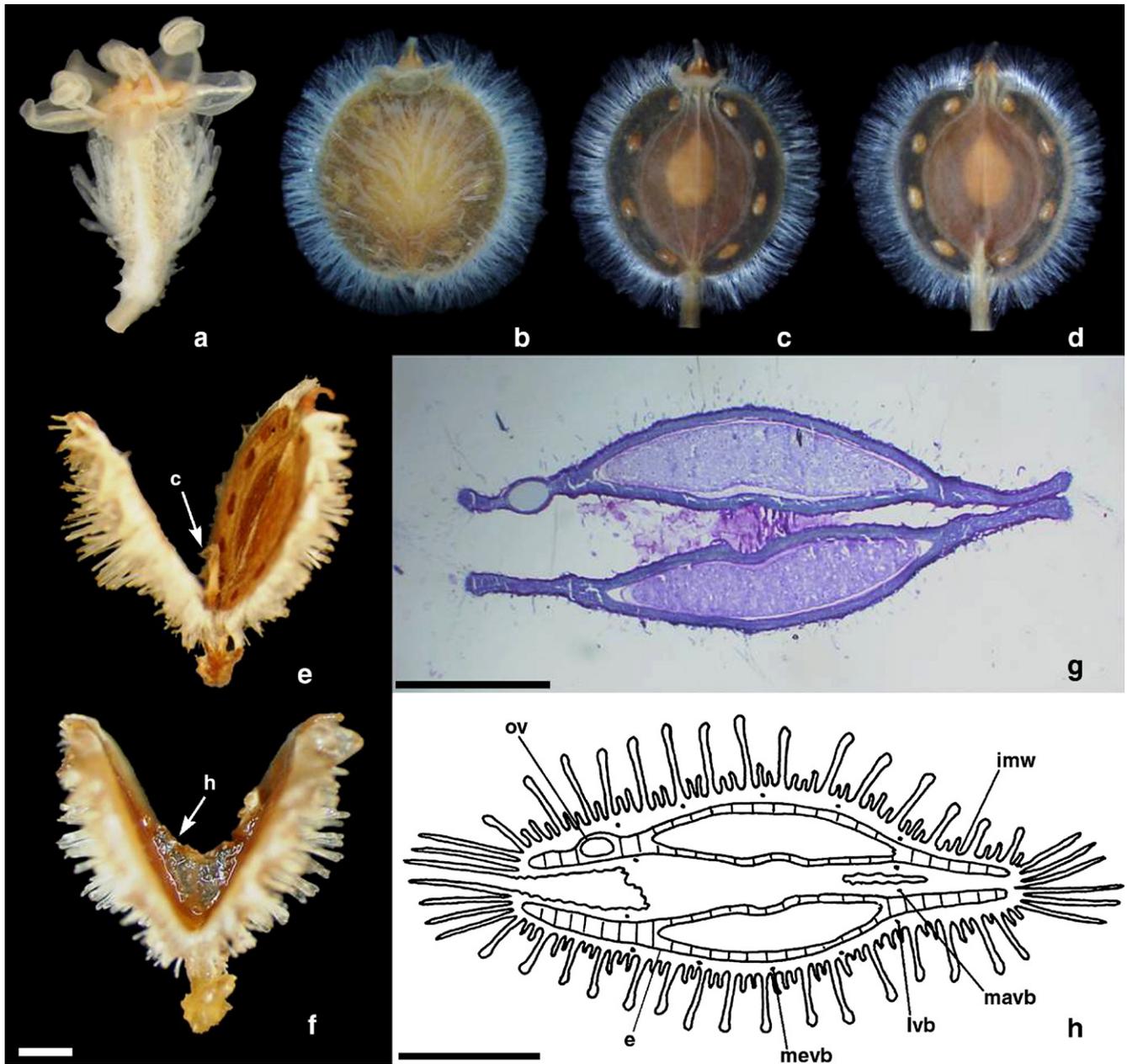


Fig. 3. A flower (a) and several fruits (b–h) of *Choritaenia capensis*: (a) flower in lateral view. (b) Intact fruit in dorsal view. (c) Fruit with exocarp removed, showing the dorsal surface. (d) Fruit with exocarp removed, showing the commissural surface (note the short carpophore). (e) Fruit after soaking in water, with mucilage removed to reveal the short carpophore (c = carpophore). (f) Fruit after soaking in water, to show the mass of mucilaginous, hygroscopic tissue surrounding the carpophore (h = hygroscopic tissue). (g) Transverse section of fruit. (h) Drawing of transverse section of the fruit showing the vascular bundles (mevb = median vascular bundle, lvb = lateral vascular bundle, mavb = marginal vascular bundle), woody endocarp (e = endocarp), oil vesicles (ov = oil vesicles), fruit wings (imw = inter-rib marginal wings) and surface vestiture (all from Smith 540, PRE). Scale bar=1 mm.

are also no vittae. A rare and distinctive feature of *Choritaenia* fruits is the presence of a variable number (four to six in each wing) of globose oil vesicles, situated at regular intervals in the wings (Fig. 3c, d). The endocarp is woody (Fig. 3h), the commissure (the area where the two mericarps are joined) is very wide and covers the entire width of the mericarp (Fig. 3g, h), and crystals are absent. Unlike most other Apiaceae, *Choritaenia* has no ventral bundles or conventional carpophores (Fig. 3d, g, h). The carpophore is represented by a short structure present at the base of the fruit only (Fig. 3d–f). It does not

extend beyond the lower part of the fruit, perhaps up to the middle. This unusual carpophore is bipartite from the base and becomes markedly swollen when moistened, presumably as a mechanism to separate the mericarps and facilitate their dispersal after rain.

4. Discussion

The unusual combination of morphological characters found in *C. capensis* is unique in the family. No other genus or species

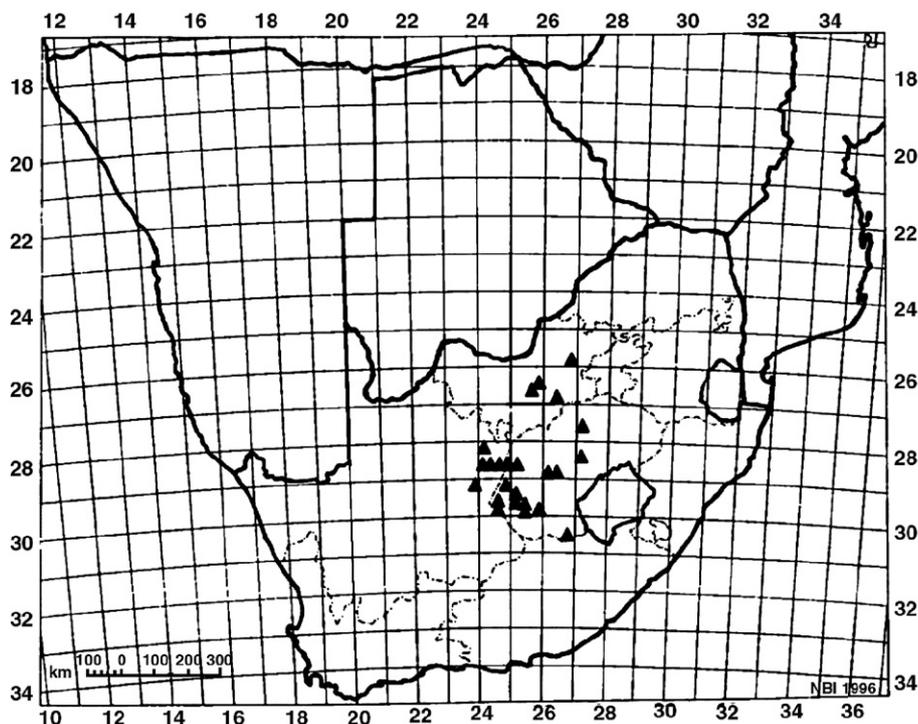


Fig. 4. The known geographical distribution of *Choritaenia capensis* (▲).

combines a woody endocarp with “inter-rib” marginal wings and oil vesicles. The wings are situated between the lateral and marginal vascular bundles and, since ribs are absent, should perhaps rather be referred to as “inter-bundle” marginal wings. “Inter-bundle” ribs or wings are also found in the tribe Laserpitieae Benth. but these genera and species all have four ribs or wings and not only two per mericarp. A woody endocarp is found in the subfamilies Azorelloideae and Mackinlayoideae but in Azorelloideae the fruits have lateral or marginal wings and in Mackinlayoideae are laterally compressed. Discrete oil vesicles are extremely rare in the Apiaceae and as far as we know are present only in the genus *Smyrniopsis* Boiss. (tribe Smyrnieae Spreng.), where they occur irregularly around the seed. Such vesicles occur elsewhere only in the genera of the Myodocarpaceae (personal observations and Lowry, 1986). *Choritaenia* is clearly different from all other genera of the Apiaceae, and shares only a woody endocarp with genera of Azorelloideae (former “hydrocotyloids”). Its phylogenetic relationships within the family therefore remain obscure.

5. Taxonomy

5.1. *Choritaenia*

Benth. in Benth. and Hook.f., Gen. Pl. 1: 907 (1867); Burt Davy in Ann. Transvaal Mus. 3: 121 (1912); Hiroe, Umbelliferae of the World: 179 (1979); Phillips, The Genera of SA Flowering Plants: 456 (1951); Burt in Edinb. J. Bot. 48: 201 (1991); Pimenov and Leonov, Gen. Umbel.: 36 (1993).

Type species: *C. capensis* (Sond. and Harv.) Benth.

=*Pappea* Sond. and Harv. in Fl. Cap. 2: 562 (1862) *nom. illegit.*, non Eckl. and Zeyh.; Baillon, Hist. Pl. 7: 112, fig. 111

(1879); [Baillon, Nat. Hist. Pl. 7: 112–113, fig. 111 (1881)]; Drude in Pflanzenfam. 3(8): 241 (1898).

Type species: *Pappea capensis* Sond. and Harv.

The genus is monotypic and highly distinctive. It is endemic to the dry central part of South Africa (Fig. 4).

5.2. *C. capensis*

Benth. in Hook. Ic. Pl. 13: 24, t. 1231 (1877); Burt Davy and Pott-Leendertz in Ann. Transvaal Mus. 3: 121 (1912); Burt Davy, Man. Fl. Pl. Ferns Transv. 2: 521. (1932). Type: South Africa, [Free State Province], Nieuwejaarspruit, between the Gariiep and Caledon River, near the foot of the Witberg, 4–5000 ft [3026DB], Zeyher *s.n.* sub Herb. Hook. (K!, lectotype, designated here). [Note: The specimen with the locality “Nieuwejaarspruit” is the only original Zeyher material available in Kew, where Bentham (and Hooker) was based].

P. capensis Sond. and Harv. in Fl. Cap. 2: 562 (1862), *non* Eckl. and Zeyh., *nom. illeg.* Type as above.

Annual, compact, prostrate herb, (0.05–) 0.1–0.2 (–0.35) m diameter and less than 25 mm high, very floriferous. Leaves small, irregularly and subternately dissected, basal relatively long, up to 28 mm long, upper much smaller, 5–8 mm long. Umbels small, from base to apex of branches, single or up to three, peduncle absent; bracts foliaceous, 3–5 mm long, resembling leaves; bracteoles foliaceous, 1.0–2.5 mm long, resembling leaves. Calyx lobes short, ovate. Petals white (or purplish?). Fruit orbicular, compressed, somewhat biconvex, 3–5 mm long, crowned with persistent disc and styles, with two “inter-rib” marginal wings (wings not associated with vascular bundles), covered with stiff, club-shaped hairs but with longer, thin hairs along margins; mericarps not separating when dry but

splitting apart when wet; commissure very broad. *Endocarp* woody. *Carpophore* highly modified, upper part reduced to soft tissue, lower part short, thick, hygroscopic, myxogenic. *Ribs* absent. *Vittae* and rib oil ducts absent, but with globose oil vesicles at regular intervals in wings. *Crystals* absent.

5.3. Distribution, habitat and phenology

C. capensis has a fairly wide distribution in the dry interior of South Africa (Fig. 4). It appears to be restricted to the Northern Cape, North–West and Free State Provinces. Burt Davy (1932) mentions Bechuanaland (now Botswana) as a locality, but we have not seen any material from this country. Plants are usually recorded from disturbed places such as roadsides, dry dams and flood plains. Flowering occurs in the spring and early summer, mainly September and October, but specimens have been collected as early as June and as late as January. The unusual features of the fruits – the dense vestiture and hygroscopic carpophore – appear to be an adaptation to allow a quick response to the first (early) spring rains in the predominantly summer rainfall region.

5.4. Additional material examined

North West Province:

- 2526 (Zeerust): Panfontein Game Reserve (-DD), 10 October 1951, Louw 1974 (PRE).
- 2625 (Delareyville): Biesiesvlei (near Sannieshof) (-BD), 21 January 1987, Retief 1800 (PRE); District Lichtenburg, farm Tweelingspruit (-BD), 7 November 1948, Kinges 1937 (PRE); Barberspan Nature Reserve (-DA), 15 October 1974, Zambatis 699 (PRE); Hieromdraai, near Barber's Pan (-DA), 2 October 1921, Pole-Evans 208 (PRE).
- 2626 (Klerksdorp): Klerksdorp, Wolwerand (-CD), 4 September 1972, Hanekom 1834 (K, PRE).

Free State Province:

- 2727 (Kroonstad): Kroonstad, vlei near pumping stations (-CA), October 1928, Pont 435 (PRE).
- 2824 (Kimberley): Kimberley, Alexandersfontein (-DB), October 1947, Brueckner 945 (PRE).
- 2825 (Boshof): Smitskraal (-CA), 4 September 1911, Burt-Davy 10751 (PRE).
- 2826 (Brandfort): Bloemfontein, Krugersdriftdam Nature Reserve, at Deelhoek (-CC), 24 September 1974, Muller 1420 (PRE); District Bloemfontein, Glen (-CD), December 1924, Heyink s.n. sub PRE 48590 (PRE); Glen Agricultural College (-CD), 19 September 1988, Zietsman 271 (PRE).
- 2827 (Senekal): Willem Pretorius Game Reserve (-AC), 28 October 1969, Edwards and Scheepers 4145 (PRE).
- 2924 (Hopetown): Modder River flats, Poplar Grove Bridge, Jacobsdal district (-BB), 7 September 1963, Acocks 23339 (K); Fauresmith district, 11 miles west of Luckhoff (-DA), 11 June 1948, Acocks 14345 (PRE); Luckhoff district, Klein

Grys Kop Farm No 445 (-DC), 3 September 1925, Smith 486 (PRE).

- 2925 (Jagersfontein): Fauresmith district, Goede Hoop Farm in the Koffiefontein area (-AC), 10 September 1927, Smith 4511 (PRE); Fauresmith district, Bremlea Farm, about 18 miles W by NW of Fauresmith (-CA), 18 August 1927, Smith 4335 (PRE); Fauresmith district, Groenvlei (-CB), October 1935, Verdoorn 1647 (K, PRE); Fauresmith district, near Fauresmith Station (-CB), 4 September 1925, Pole Evans and Smith 1797 (PRE), 3 September 1925, Smith 540 (PRE), October 1925, Smith 978 (BM, K); Fauresmith Veld Reserve (-CD), 21 August 1934, Henrici 2653 (PRE); Edenburg district, farm "The Meadows", 7 miles south of Edenburg (-DD), 24 October 1927, Smith 4624a (PRE).

Northern Cape Province:

- 2824 (Kimberley): Barkley West district, Vaalbos National Park (-AD), 20 October 1988, Zietsman 427 (PRE); Kimberley, Middelplaats (-CA), 15 September 1936, Esterhuysen s.n. sub PRE 700482 (PRE); Barkley West district, Pniel (-CB), 16 September 1936, Acocks 713 (PRE), Pniel (-CB), 8 October 1936, Acocks s.n. sub Herb. Häfstrom 813 (PRE); 15 miles from Kimberley on Samaria road (-DA), September 1947, Brueckner 912 (PRE); 7 miles W of Kimberley off Schmidtsdrift road (-DA), 31 July 1960, Leistner 1979 (K, PRE).
- 2923 (Douglas): Herbert district, St Clair, near Douglas (-BB), "August 1926", MacOwan 3360 (SAM), August 1896, MacOwan 1881 (BM), MacOwan s.n. (K), Orpen 1881 (K, PRE), September 1897, Orpen 34 (PRE).
- Without precise locality: Griqualand West, M.E. Barber 12/76 (K).

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