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A taxonomic revision of the Othonna auriculifolia Less. group (Asteraceae: Senecioneae: Othonninae)

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A taxonomic revision is presented for the two geophytic species of Othonna L. (Asteraceae: Senecioneae: Othonninae) distinguished by a condensed caudex without evident internodes. These species are morphologically and phylogenetically distinct from the remaining geophytic species. This account includes descriptions, complete nomenclature and typification, illustrations and geographical distribution. We recognise the following two species: O. auriculifolia with radiate capitula and mature pappus 3-25 mm long, and O. taraxacoides (DC.) Sch. Bip. with disciform capitula and mature pappus 3-8 mm long. Both species are vegetatively variable.

Keywords: geophytes; Othonna auriculifolia; O. taraxacoides; nomenclature; southern Africa; synonyms; succulent.

Introduction

The genus Othonna L. (Asteraceae, Senecioneae, Othonninae) comprises ± 90 species of succulent or sub-succulent perennial herbs or shrubs with moreor-less dorsiventrally flattened leaves and radiate or disciform capitula with female-sterile disc florets and female marginal florets with a beige or reddish pappus that is sometimes accrescent (Leistner 2001; Nordenstam 2007, 2012; Magoswana et al. 2019). The genus is concentrated in the Greater Cape Floristic Region of South Africa but extends into southern Namibia, southern Angola and Zimbabwe (Manning & Goldblatt 2012; Manning 2013; Magoswana et al. 2019, 2020).

The genus was last revised in its entirety by Harvey (1865) and is in urgent need of a modern taxonomic revision, although the preliminary floristic treatments by Manning and Goldblatt (2012) and Manning (2013), as well as the recent taxonomic revision of the geophytic species of the genus by Magoswana et al. (2019), constitute a valuable contribution to a complete revision of the genus in the Greater Cape Floristic Region.

Phylogenetic and biogeographic relationships within Othonna have not yet been adequately analysed, although the monophyly of the genus and its systematic position in the tribe Senecioneae have been established (Pelser et al. 2007). Preliminary molecular analyses (Magoswana 2017, unpubl.) retrieved the species with a tuberous rootstock and well-developed stem with cauline leaves in a clade comprising the majority of the geophytic species but excluding the remaining few geophytic species with a rosulate habit and condensed caudex.

The geophytic species with an aerial stem (the O. bulbosa group) were recently monographed by Magoswana et al. (2019). The present account serves to complete the taxonomic treatment of the geophytic species of the genus Othonna, viz. with a rosulate habit (hereafter termed the O. auriculifolia group). Members of the O. auriculifolia group are deciduous geophytes with the crown at or near ground level and the annual stem highly condensed without evident internodes, thus appearing unbranched. The leaves and branches originate directly from the crown of the subterranean tuberous root, and the capitula are sub-scapose. The flowering capitula are erect or suberect, but the scapes become decumbent in fruit, with the capitula flexed upwards. In contrast, the O. bulbosa group have the crown or growth point of the subterranean rootstock with its renewal buds buried well below the soil surface, thus with the lower portion of the annual flowering stem underground and the exposed portion usually well developed. The fruiting peduncles remain erect in fruit (Magoswana et al. 2019).

We provide complete nomenclature and typifications, detailed descriptions and illustrations, and geographical distribution for both species of the *O. auriculifolia* group. Two species are recognised (*O. auriculifolia* Less. and *O. taraxacoides* (DC.) Sch. Bip.), and five names are reduced to synonymy.

Research methods and materials

Procedures

All relevant types were examined, as well as all collections from BOL, NBG, PRE and SAM (acronyms following Thiers 2022), the primary collections of southern African species. If the collecting number was not cited in the protologue but is present on the actual specimen then we have included this number in square brackets following the collector's name. Measurements of vegetative and reproductive structures were taken from specimens across the distribution range of each species to account for variation between the subpopulations. For leaf characters, only well-developed lower leaves were measured, as upper leaves may grade into bracts. Leaf width was measured at \pm the middle of the leaf and leaf length did not include the petiole (if the species has a petiole).

The capitula were initially rehydrated for an hour in pre-boiled water and subsequently the involucral bracts and florets (ray and disc), anthers and stigmas were excised and studied under an Olympus SZ61 stereomicroscope and photographed using an Olympus SC30 camera with Olympus analysis getIT soft imaging

software (Informer Technologies, Inc.). Species localities are cited following the Quarter Degree Reference System (Edwards & Leistner 1971; Leistner & Morris 1976). Both species were also studied in the field in both the Northern and Western Cape provinces of South Africa over the winter and spring growing periods. During these field visits, photographs and detailed field notes were taken to capture any features lost when specimens were pressed, as well as information on habitat, flowering time and species associations.

Taxonomic treatment

Othonna L., Species Plantarum 2: 924. (1753). Type: O. coronopifolia L., lecto., designated by Green: 184 (1929).

Doria Thunb., Nova Genera Plantarum 12: 162. (1800). Type: Not designated.

Shrubs, subshrubs, or geophytes with underground tuber or herbs, ± succulent, crown and leaf axils cobwebbed. Leaves alternate, sometimes crowded basally, linear to ovate or obovate-spatulate or lyrate to pinnatisect, sub-succulent or leathery. Inflorescence terminal, pedunculate, capitula solitary or laxly cymose or paniculate. Capitula heterogamous, radiate or disciform. Involucre campanulate, bracts uniseriate, free and adherent or connate up to 1/2, lanceolate to oblong, glabrous, green with scarious margins. Receptacle conical, punctate, glabrous, epaleate. Marginal florets female-fertile, usually yellow or sometimes white, rarely pink to mauve, filiform or ligulate; ovary glabrous or appressed-puberulous with white twin hairs; style branches with discrete lateral stigmatic areas, apices oblanceolate and shortly papillate. Cypselas ellipsoid to obovoid, 10-ribbed, dark brown, densely appressed-puberulous with myxogenic or non-myxogenic white twin hairs, rarely glabrous; pappus bristles many, basally united, barbellate, persistent, beige or sometimes banded deep red. Disc florets functionally male, numerous, yellow or white to blue or pink, corolla tube funnel-shaped, 5-lobed; anthers obtuse at base with ovate apical appendages, filament collar balusteriform; ovary glabrous; style simple and conetipped, rarely with short branches but then without lateral stigmatic zones; pappus of ± 10 barbellate bristles, sometimes reduced to one or two bristles and lacking in one species, united basally, white.

Distribution and ecology: ± 90 spp., largely restricted to the Greater Cape Floristic Region, with a few species in the eastern summer rainfall regions of South Africa and some extending to southern Angola and Zimbabwe; usually on sandy flats or rocky slopes, rarely seasonally damp sandy flats.

Key to the species of the Othonna auriculifolia group

- 1a. Shrubs or shrublets, succulents without tuberous rootstock remaining species of *Othonna*
- 1b. Geophytes with thickened or tuberous rootstock:
- 2b. Crown at or near ground level, annual stem highly condensed without evident internodes, appearing unbranched; leaves originate directly from crown of subterranean tuberous root:
- 3a. Capitula disciform; pappus of marginal florets 3–8 mm long . . . 1. *O. taraxacoides* (DC.) Sch. Bip.
- 3b. Capitula radiate; pappus of marginal (ray) florets 6–25 mm long 2. *O. auriculifolia* Less.

Species treatments

1. Othonna taraxacoides (DC.) Sch.
Bip. in Flora 27(2): 769 (1844). Doria
taraxacoides DC., Prodromus 6: 471
(1838); Harv. in Flora Capensis. 3: 325
(1865). Type: South Africa, [Northern
Cape]: 'in Africæ Capensis regione
Gariepinâ' [Zwischen Zilwerfontein,
Kooperbergen und Kaus in Drège
(1843)], Drège [2881] [Sept.—Oct.
1838] (G-DC-G00473781, holo.—
image!; K-000307012—image!,
P-0010014—image!, iso.).

Deciduous geophyte, to 150 mm, stem subterranean, condensed, appearing unbranched, felted at crown; rootstock cylindrical to oblong. Leaves emergent or fully developed at flowering, crowded basally, erect to spreading, base narrowed and petiole-like, blade obovate-spatulate or rarely lyrate-pinnatifid, $10-35 \times$ 5-25 mm, undulate-incised or crenate, glabrous, glaucous, petiole 5-50 mm long. Inflorescence cymose but appearing sub-scapose, one or more capitula per plant; scapes erect at flowering but decumbent in fruit, 20-100 mm long, glabrous, ebracteate or sometimes with one or two bracteoles near base. Capitula disciform, involucre 10-20 mm diam., involucral bracts 13 or 14, lanceolate to elliptic, $5-15 \times 2-4$ mm, glabrous-penicillate. Marginal florets 13 or 14, corolla tube reduced, collar-like, 0.5-1.5 mm long, pale to deep yellow; ovary ellipsoid-ovoid; style bifid, greatly exserted, 4-6 mm long. Cypselas ellipsoid-ovoid, $2-4 \times 1-2$ mm, densely appressed-puberulous on ribs with white myxogenic twin hairs; pappus of numerous barbellate bristles, 3-8 mm long, beige or sometimes deep red. Disc

florets numerous, yellow, corolla funnel-shaped, tube \pm as long as limb, 0.5–2.0 mm long; filaments 1–2 mm long; ovary narrowly ellipsoid, 3–8 mm long, glabrous; style simple and cone-tipped; pappus of \pm 10 barbellate bristles united basally. Figure 1A, B.

Distribution and ecology: a local endemic of the winterrainfall region of Northern Cape, South Africa, distributed along the western escarpment from the Richtersveld to the Kamiesberg Mountains; usually in patches of gravelly quartz or sometimes in quartz outcrops, rarely on granite substrates. Flowering from July to September (Figure 2).

Diagnosis: Othonna taraxacoides is an acaulescent geophyte with obovate-spatulate or lyrate-pinnatifid leaves 10–35 mm long, and sub-scapose, disciform capitula (Figure 1A, B). The pappus of the cypselas is invariably short, 3–8 mm long.

Conservation status: The species is classified as Least Concern (LC) in the SANBI Red List of South African Plants (von Staden 2016).

Additional specimens examined

SOUTH AFRICA. Northern Cape: Vioolsdrif (2817): Richtersveld (–AC), Sept. 1933, Herre s.n. (NBG); base of Umdaus (–DC), 1 Aug. 1988, Williamson 3915 (NBG). Springbok (2917): Steinkopf, W of town along highway (–BA), 22 Aug. 2015, Deacon 4448 (NBG); 15 km N of Steinkopf (–BA), Sept. 1995, Williamson 5699 (NBG); 3 miles (5 km) W of Steinkopf (–BA), Aug. 1949, Hall s.n. (NBG); ± 10 km E of Jakkalswater (–BB), 8 Jul. 2008, Bruyns 11116 (NBG); 12 miles (19 km) E of Springbok (–DB), 25 Aug. 1954, Barker 8382 (NBG). Gamoep (2918): Kweekfontein (–CA), 2 Aug. 2000, Bruyns 8239 (NBG). Hondeklipbaai (3017): Kamieskroon (–BB), 4 Aug. 1952, Hall NBG 462/52 (NBG). Kamiesberg (3018): eastern Kamiesberg between Paulshoek and Platbakkies (–AD), 8 Sept. 2006, Snijman 2088 (NBG).

2. Othonna auriculifolia Less. in Linnaea 6: 93 (1831) [as 'auriculaefolia']; DC., Prodromus 6: 481 (1838); Harv. in Flora Capensis 3: 340 (1865). Type: South Africa, [?Northern Cape]: 'Roggeveld Majo', without date, *Lichtenstein s.n.* in Herb. Willdenow 16734 (B-W 167340 -10, holo.—image!). [Note: The name has until now been cited as 'Licht. ex Less.' based on Lessing's (1831) citation of the taxon as 'O. auriculaefolia Lichtenstein in herb. W. No. 16734' but we find no evidence that Lichtenstein used this name and interpret this entry as merely a citation of the type specimen.]

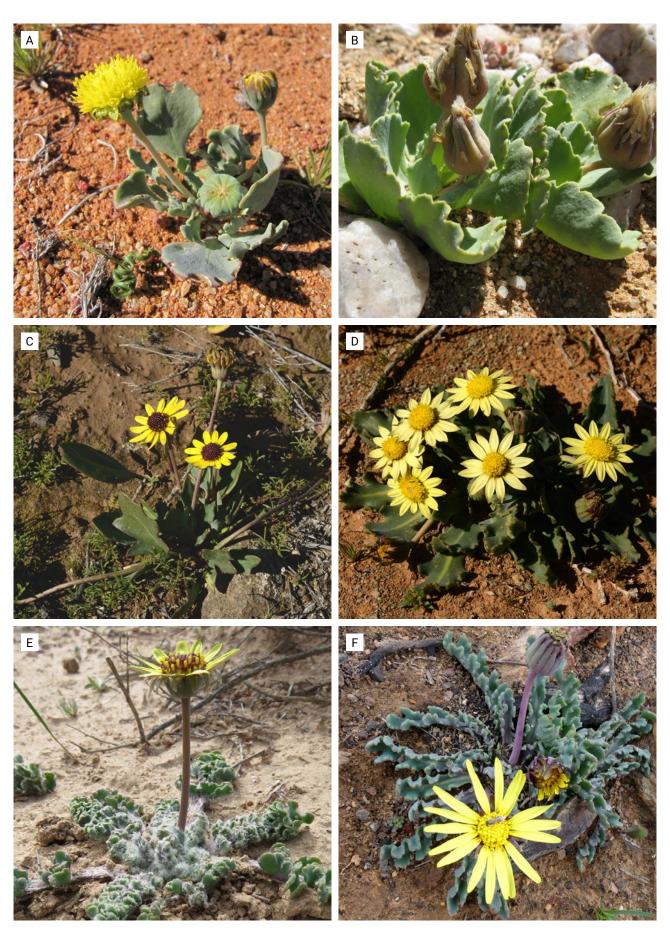


Figure 1. General morphology. A, B, habit of *O. taraxacoid*es showing obovate-spatulate or lyrate-pinnatifid leaves and disciform capitula; C–F, *O. auriculifolia*, note the leaves densely covered with long tangled hairs (E), and capitula with 17 ray florets (F). Photographs: A,B: J. Manning; C, E. Marinus; D, F. Linde; E,F: N. Helme.

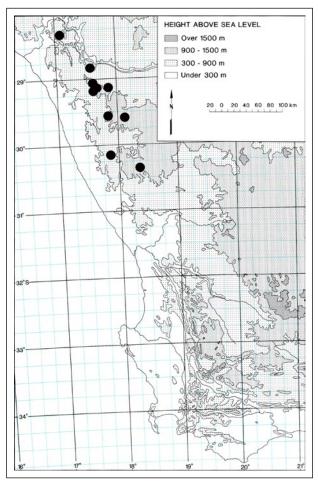


Figure 2. Distribution of O. taraxacoides.

Othonna cyanoglossa DC., Prodromus 6: 481 (1838). Type: South Africa, [Western Cape]: 'Carro, Pietermeintjesfontein' [Matjiesfontein], June 1838, Drège [6078] (G-DC, holo.-microfiche!, P-0004607—image!, syn.).

Othonna lactucifolia DC., Prodromus 6: 482 (1838) [as 'lactucæfolia']. Type: South Africa, [Eastern Cape]: 'in Africa Capensi ad Graaf-Reynet' [Graaff-Reinet], Aug. 1838, Drège [6077] (G-DC, holo.—microfiche!, P-000460 image!, syn.).

Othonna picridioides DC., Prodromus 6: 482 (1838). Type: South Africa, 'in Africæ Capensi deserto Carro', Aug. 1838, Drège [6077] (G-DC-00498513, holo.—image!, P-0004605 image!, syn.).

Othonna auriculifolia var. arctotoides Harv. in Flora Capensis. 3: 340 (1865), syn. nov. Type: South Africa, 'Wolve River', May [?1842], Burke s.n., (K-0003037010, lecto., designated here; K-0003037009, isolecto.!). [Other original material: South Africa, without locality, Zeyher 992 (?TCD, not located, P-0004616image!, syn.)].

[Othonna pimulina Schltr, nom. inval. ms., non. DC., Prodromus 6: 479 (1838): Associated specimens: South Africa, [Northern Cape] 'Onder-Bokkeveld, Oorlogkloof', 21 Aug. 1897, Schlechter 10962 (BR-0000008876379 image!, BR-0000008877390, K-306927 image!, PH-20047 image!, S-08-8797)].

Deciduous geophyte, to 250 mm, stem subterranean, condensed, appearing unbranched, felted at crown; rootstock cylindrical to turnip-shaped. Leaves emergent or fully developed at flowering, crowded basally, prostrate or spreading to sub-erect, base narrowed and petiole-like or evidently petiolate, blade narrowly oblong to obovate or suborbicular, flat or concave with lobes curled up, $20-120 \times 5-25$ mm, serrate or pinnatisect with quadrate to rounded lobes, or rarely entire, leathery to sub-succulent, usually glabrous, sometimes ciliate basally, or rarely sparsely to densely lanate or stiffly setose on both surfaces, glaucous or spotted or streaked with purple, petiole 10-80 mm long. Inflorescence cymose, appearing sub-scapose, one to several capitula per plant; scapes erect at flowering but decumbent in fruit, 20-180 mm long, glabrous or rarely sparsely lanate and glabrescent, bracteate basally with 1 or 2 lanceolate to elliptic or sometimes leaf-like bracts. Capitula radiate, involucre 10-30 mm diam., involucral bracts 11 to 14, lanceolate to elliptic, $7-15 \times 2-5$ mm, glabrous-penicillate or rarely lanate. Marginal florets 11 to 14(17), corolla tube reduced, collar-like or cylindrical, 0.5-2.0 mm long, limb lanceolate to elliptic, 7-15 mm long, unicolorous or discolorous, pale to deep yellow above, usually flushed purple or blue beneath; ovary ellipsoid to obovoid; style bifid, included, branching below mouth of tube. Cypselas ellipsoid-ovoid, $2-6 \times 1-3$ mm, densely appressed-puberulous on ribs with white myxogenic twin hairs; pappus of numerous barbellate bristles, 3-25 mm long, united basally, beige. Disc florets numerous, yellow or lobes sometimes mauve to purple, corolla funnel-shaped, tube \pm as long as limb, 0.5–2.0 mm long, lobes lanceolate to ovate, 0.5-1.0 mm long; filaments 1-2 mm long; ovary narrowly ellipsoid, 2-6 mm long, glabrous; style simple and cone-tipped; pappus of \pm 10 barbellate bristles united basally. Figure 1C-F.

Distribution and ecology: a well-collected species that is widely distributed through the drier interior parts of southwestern and western South Africa, where it is best known from the Hantam and Roggeveld in Northern Cape but as far north as Springbok, extending along the drainage basin of the Orange River into Bushmanland, and south through the interior Cape Floristic Region of Western Cape to Willowmore in Eastern Cape, with scattered records from the interior parts of Eastern Cape and southern Free State; occurring on a wide variety of substrates, usually on shale flats in open karroid scrub, rarely on sandy flats or on sandstone rock sheets at high altitudes in arid fynbos. Flowering from May to September (rarely early October at high altitude) (Figure 4).

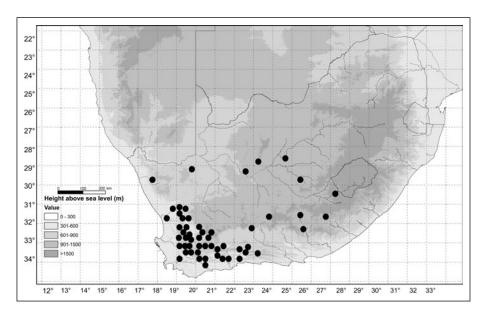


Figure 3. Distribution of *O. auricu-lifolia*

Diagnosis: Othonna auriculifolia is an acaulescent geophyte with entire or serrate to pinnatisect leaves and scapose, radiate capitula with 11 to 14 involucral bracts and often discolorous ray florets, and disc florets sometimes with mauve to purple lobes. The species is vegetatively variable, the leaves ranging from narrowly oblong to obovate and pinnatisect to serrate or sometimes entire and suborbicular (Figures 1C-F & 4). The leaves of O. auriculifolia are usually glabrous but a few populations between Clanwilliam and Calvinia [Coetzee CJ1 (NBG), Koopman DK049 (NBG) and Schlechter 10836 (BOL)] are distinctive in having the leaves densely covered with long, tangled hairs. We considered the possibility that these populations represent a separate species but additional populations from Worcester [Tyson s.n. (SAM)] are sparsely lanate-glabrescent and thus intermediate between the glabrous and densely hairy plants, and populations on the Hex River Mountains have the leaves stiffly setose. We therefore conclude that Othonna auriculifolia is also variable in leaf vestiture.

Candolle (1838) treated a number of these vegetative variants as distinct species. Othonna cyanoglossa DC., based on a collection from Matjiesfontein in Western Cape, was distinguished by ovate to sub-rotund leaves with sinuate-dentate margins, and scapes ± as long as the leaves; O. lactucifolia DC., from Graaff-Reinet in Eastern Cape, by ovate leaves with sinuate, mucronate-dentate margins and peduncles as long as the leaves; and O. picridioides DC. from the 'Karoo' by pinnatifid leaves with subrotund lobes with serrate-dentate margins, and peduncles shorter than the leaves. These taxa were synonymised by Harvey (1865), a decision that is supported by our observations of the ± continuous variation in leaf shape among collections and sometimes even individual plants, as well as observations in the field. Harvey (1865), however, segregated plants from Wolve River near Calvinia in

Northern Cape with petiolate, cuneate-obovate leaves with entire or repand, or sometimes variably incised or pinnatifid margins, as var. *arctotoides* Harv. Specimens matching this form occur throughout the range of the species among more typical individuals, and evidently represent extreme or juvenile variants, and we do not recognise the variety.

Conservation status: The species is classified as Least Concern (LC) in the SANBI Red List of South African Plants (Raimondo et al. 2009).

Additional specimens examined

SOUTH AFRICA. Free State: Jagersfontein (2925): Fauresmith Botanical Reserve (–CB), 1 Sept. 1925, Smith 398 (PRE); 2 Sept., 1925, Smith 418 (PRE); 27 Jul. 1930, Potter 2022 (PRE); 1 Sept. 1925, Pole-Evans and Smith 841 (PRE).

Northern Cape: Griekwastad (2823): Griquatown (-CC), Jun. 1895, Marloth s.n. (PRE); Jul. 1914 (PRE). Kimberley (2824): 7 miles [11 km] NE of Kimberley on Samaria Road (-DA), 24 Aug. 1961, Leistner and Joynt 2649 (PRE); 3 miles (5 km) N of Kimberley (-DA), 17 Jun. 1959, Leistner 1421 (PRE). Springbok (2917): Hester Malan Nature Reserve (-DB), 1 Jul. 1975, Rosch and Le Roux 1167 (PRE). **Pofadder** (2919): Farm Gannapoort, 26 miles [42 km] east of Pofadder (-BC), 21 May 1961, Schlieben 8952; Leistner 2470 (PRE). Prieska (2922): Prieska (-BC), Jun. 1935, Bryant 1130 (PRE). Calvinia (3119): Bokkeveld, Farm Meulsteenvlei (-AC), 13 Sept. 1926, Marloth 12945 (PRE); Nieuwoudtville (-AC), 11 May 1983, Perry and Snijman 2093 (NBG); 15 Jun. 1983, Perry and Snijman 2112 (NBG, PRE); 8 Sept. 1983, Perry and Snijman 2356 (PRE); 15 Sept. 2000, Koekemoer and Funk 1949 (PRE); ± 3 km S of Nieuwoudtville (-AC), 4 Jun. 2010, Helme 6584 (NBG); Glen Ridge Farm, Nieuwoudtville (-AC), 19 Jul. 1962, Barker s.n. (NBG); Nieuwoudtville, Hantam National Botanical Gardens (-AC), 13 May 2015, Coetzee CJ1 (NBG); 23 May 2016, Koopman DK049 (NBG); Willem's River (-AC), without date, Leipoldt 754 (SAM); Karigaboschfontein S of Calvinia (-AD), 20 Aug. 1975,



Figure 4. Leaf variation in *Othonna auriculifolia*. A, suborbicular blade with entire margins; B, obovate blade with sparsely serrate margins; C, pinnatisect leaves; D–G, serrate leaves with quadrate lobes; H, densely or stiffly setose, pinnatisect leaves. Scale bar: 2 cm.

Thompson 2473 (NBG); foot of Hantam Mountains (–BC), Jul. 1948, Lewis 2586 (SAM); Hantamsberg, summit of plateau above Ambralshoek (–BD), 18 Aug. 1975, Thompson 2336, 2338 (NBG); Menzieskraal 816, 35 km SE of Nieuwoudtville on Botterkloof Road (–CA), 11 Aug. 2009, Helme 6450 (NBG); Nieuwoudtville Nature Reserve (–CA), 8 Sept. 1983, Perry and Snijman 2356 (NBG); 7 Aug. 1986, Steiner 1243 (NBG); Kareeboomfontein (–DA), 5 Sept. 1974, Hanekom 2398 (PRE); Riepjoeni [Rebunie] Mountains (–DA), Aug. 1921, Marloth 10301 (PRE). Victoria West (3123): Groot Boschmanspoort, NE

of Victoria West (–AC), 14 May 1976, Thompson 3078 (NBG). Sutherland (3220): Roggeveld, Soekop (–AA), 8 Aug. 2006, Rösch 461 (NBG); Voëlfontein Farm (–AA), 10 May 1969, Hall 219A (NBG); Tankwa Karoo National Park, top of Gannaga Pass (–AA), 5 Aug. 2006, Koekemoer 3205, 3210, 3213 (PRE); Tankwa Karoo National Park, between Quaggasfontein and Uitkyk (–AD), 7 Sept. 2013, Koekemoer 4423 (PRE); Tankwa Karoo, Quaggasfontein (–AD), 27 Sept. 1998, Desmet 1856 (NBG); Koedoesbergpas on Ceres–Sutherland Road (–CC), 20 May 1976, Hugo 398 (NBG); between Laingsburg and

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Sutherland near Komsberg Pass (-DB), 3 Jul. 1983, Vlok 609 (NBG, PRE); 3 km W of top of Komsberg Pass (-DB), 19 Jul. 2006, Bruyns 10506 (NBG).

Western Cape: Vanrhynsdorp (3118): near Vanrhynsdorp (-DA), 6 May 1965, Barker 10193 (NBG). Wuppertal (3219): Pakhuisberg, 17 km from Clanwilliam on road to Pakhuis (-AA), 25 Aug. 1995, Rodriguez-Oubina and Cruces 2101 (PRE); Pakhuis, Heuningvlei (-AA), 24 Jul. 1983, Hockey 1 (NBG); Farm Lamkraal (-AA), 14 Aug. 1897, Schlechter 10836 [2 sheets] (BOL); top of plateau, Algeria (-AC), 3 Aug. 1937, Martin NBG 1294 (NBG); Middelberg hut (-AC), Jun. 1980, Hugo 2372 (NBG); SE slopes of Bloukop (-CB), 13 Sept. 2002, Burgoyne 9340 (PRE); foothills of Bloukop on the Luiperdskloof 4 × 4 route (-CB), 11 Sept. 2002, Koekemoer 2411 (PRE); 13 Sept. 2002, Koekemoer 2425, 2430 (PRE); Breekkrans (-CB), 22 Jun. 1984, Taylor 10961 (NBG); Gonnafontein (-CB), 8 Jul. 2000, Pond UP98 (NBG); Koue Bokkeveld (–CC), 13 Aug. 1979, Miros s.n. (NBG); Groenfontein, on road to Kaggakamma (-DC), 10 Jul. 1991, Van Zyl 4205 (PRE); Knolfontein, 60 km NE of Ceres (-DC), 14 May 2008, Jardine and Jardine 870 (NBG); 26 Aug. 2012, Jardine 1818 (NBC); 29 Jul. 2009, Jardine and Jardine 1153 (NBG); 6 Sept. 2011, Jardine 1593 (NBG); 17 Aug. 2011, Jardine 1573 (NBG); 15 Jul. 2005, Jardine and Jardine 17 (NBG); 12 Sept. 2008, Jardine and Jardine 928 (NBG); 19 Jun. 2006, Jardine and Jardine 314 (NBG), 26 Jul. 2010, Jardine 1489, 1490 (NBG); 18 May 2010, Jardine 1494, 1495, 1496, 1497 (NBG); Groenfontein, Zeekoegat 137, W of Rietriver (-DC), 16 Jun. 2000, Stobie 4 (NBG). Beaufort West (3222): Courland's Kloof, Nelspoort (-DB), Jul. 1907, Pearson 1486 (SAM). Worcester (3319): Matroosberg summit (-AC), 26 Sept. 1981, Kotze 100 (NBG); Mostersthoek (-AD), 2 Aug. 1926, Stokoe 697 (PRE); Doornriver (-AD), 9 Jul. 1991, Van Zyl 4197 (NBG); Farm Tweeriviere along the Ceres-Patatsrivier Road (-BB), 25 Jun. 1979, Van Breda 4463 (PRE); Karrooport (-BC), Aug. 1919, Marloth 9010 (PRE); 27 Jul. 1941, Compton 11159 (NBG); NW of Worcester, 16 May 1948, Bayer 4142 (NBG); Hex River Mountains, N slopes of Rooiberg (-BC), 19 Aug. 1999, Oliver 11310 (NBG); 1.5 miles [2.4 km] W of Verkeerdevlei dam (-BD), 17 Jun. 1965, Acocks 23665 (PRE); Verkeerdevlei (-BD), 13 Jun. 1975, Durand 27 (PRE); 12 Jul. 1954, Barker 8287 (NBG); Matroosberg (-BD), 30 Sept. 1928, Andrea 1157 (PRE); Zachariashoek, La Motte Forest Station (-CC), 3 Jun. 1982, Viviers 386 (PRE); near Nuy (-DA), 8 Jul. 1970, Barker 10702 (NBG). Montagu (3320): Tweedside (-AB), 1 Jun. 1925, Marloth 12058, 12073 (PRE); Pieter Meintjies (-AD), 28 Apr. 1946, Barker 4023 (NBG); Klein Roggeveld (-BA), 8 Jul. 1938, Compton 7275 (NBG); Matjiesfontein, Whitehill (-BA), 7 Aug. 1933, Humbert 9726; 7 Sept. 1983, van Zyl 3567 (PRE); Whitehill (-BA), 7 Jul. 1941, Compton 10881 (NBG); 17 Aug. 1942, Compton 13385 (NBG); Waboomsberg main kloof E of Brakleegte (-CB), 14 Jul. 1994, Oliver 10484 (NBG); Touws River (-DA), Jul. 1903, Marloth 3230 (PRE); Fonteinskloof (-DC), 14 Jul. 1954, Rycroft 1590 (NBG); Barrydale (-DC), 5 Aug. 1949, Barker 5463 (NBG); 6 Aug. 1949, Barker 5400 (NBG). Ladismith (3321): N of Klein Swartberg (-AD), 24 Jul. 1957, Warts 1508 (NBG); Gamka Mountain (-BC), 20 Aug. 1975, Boshoff P223 (NBG); Witteberg (-CA), 11 May 1941, Compton 10813 (NBG); top of Witteberge, Matjiesfontein (-CA), 29 Sept. 1983, Van Zyl 3566 (NBC);

Derde River (-CD), 8 Jun. 1925, Muir 3624 (PRE); N of Garcia's Pass (-CC), Sept. 1923, Muir 2951 (PRE); Farm Phisante Kraal 166, top of Witteberg (-CC), 9 Aug. 1988, Pool 57 (NBG); \pm 1 km along road from Dwars in die weg to Rietkuil (-DA), 5 Aug. 2015, Manning and Magoswana 3507 (NBG); Gamka Mountain Reserve, Bakenskop (-DB), 16 Apr. 1998, Rourke 2127 (NBG, PRE); Gamka Mountains between Calitzdorp and Oudtshoorn (-DB), 22 Jul. 1980, Taylor 10209 (PRE); Gamka Mountain Reserve (-DB), 16 Apr. 1998, Rourke 2127 (NBG); Mountain Zebra Reserve, between Calitzdorp and Oudtshoorn (-DB), 22 Jul. 1980, Taylor 10209 (NBG). Oudtshoorn (3322): Farm Frisgewaagd, Swartberg Mountains (-AD), Jun. 1986, Vlok 1486 (PRE); Vrolikheid (-BC), Jul. 1976, Merwe 2837 (PRE); Oudtshoorn commonage (-CA), Jul. 1925, Marloth 12180 (PRE); Farm Kleinvlakte, 10 miles [16 km] from Barrydale (-DC), 3 Jun. 1974, Van Breda 4240 (PRE). Bredasdorp (3420): Rietvallei, on boundary of four farms and Suurbraak (-BA), 17 Aug. 2008, Von Witt CR3209 (NBG).

Eastern Cape: Lady Grey (3027): Fontein's Kloof, near Driefontein (-CD), 14 Jul. 1954, Lewis 4497 (SAM). Victoria West (3123): Murraysberg (-DD), Apr. 1879, Tyson 390 (PRE). Steynsburg (3125): Conway farm (-CB), Aug. 1899, Gilfillan 5552 (PRE). Queenstown (3126): N slopes of Andriesberg (-DA), 23 May 1899, Galpin 2611 (PRE). Cradock (3225): National Bergkwagga Park [Mountain Zebra National Park] (-AD), 5 May 1963, Liebenberg 7214 (PRE). Willowmore (3323): Uniondale, Vettevlei (-CA), 8 Jul. 1935, Markötter s.n. (NBC).

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Author contributions

S.L.M. and J.M. were the project leaders, A.M. and J.S.B. made conceptual contributions.

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