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# *Triandra pellabergensis* (Hyacinthaceae subfam. Urgineoideae), a new genus and species from Pella se Berge, Northern Cape Province, South Africa

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#### Abstract

Within the framework of a taxonomic revision of subfamily Urgineoideae based on morphological, genetic and phytogeographic data covering numerous samples from its whole range of distribution, we here describe a new genus and species from Pella se Berge in northwestern South Africa. *Triandra* gen. nov. is easily characterized by the absence of stamens associated with the outer tepal whorl, therefore having only three stamens per flower, a character previously unknown in Hyacinthaceae. *Triandra pellabergensis sp. nov.* produces hypogeal bulbs with filiform proteranthous leaves, spurred bracts, lax racemes with few, nodding, nocturnal flowers and erect capsules with the withered tepals persisting atop. The new species resembles *Urginea revoluta* in general morphology, although this latter species has six stamens per flower, a different seed morphology, a distinct phytogeographic pattern, and a distant phylogenetic relationship. A complete morphological description is presented for the new genus and species, including data on its biology, ecology and distribution.

Keywords: Asparagaceae, Drimia, Urginea, Scilloideae, taxonomy, distribution

#### Introduction

Family Hyacinthaceae comprises about 1000 species of bulbous plants mostly distributed in Africa, Europe and Asia, with a single genus, *Oziroë* Rafinesque (1837: 53), present in South America (Speta 1998a, 1998b, APG 2003). Within Hyacinthaceae, four monophyletic subfamilies are accepted: Hyacinthoideae, Ornithogaloideae, Oziroëoideae and Urgineoideae (Speta 1998b, Pfosser & Speta 1999, Manning *et al.* 2004, Martínez-Azorín *et al.* 2011). Alternatively, Hyacinthaceae is treated as Asparagaceae subfamily Scilloideae, and consequently the former subfamilies are reduced to the tribes Hyacintheae, Ornithogaleae, Oziroëeae and Urgineeae (APG 2009, APG 2016, Chase *et al.* 2009); we favour the former treatment based on morphology.

Generic circumscription of Urgineoideae has been especially controversial in recent decades (Martínez-Azorín *et al.* 2013, 2017, 2018a, 2019a, 2019b, Pinter *et al.* 2013, Crouch & Martínez-Azorín 2015). On the one hand, Manning *et al.* (2004) presented a radical treatment, recognising only two genera for the whole subfamily: *Bowiea* Harvey ex Hooker (1867: t. 5619) and *Drimia* Jacq. ex Willdenow (1799: 165), the latter being extremely broad in morphology and including in synonymy several traditionally accepted genera which are identified by unique syndromes of morphological characters, such as *Litanthus* Harvey (1844: 314), *Rhadamanthus* Salisbury (1866: 37), *Rhodocodon* Baker (1880: 280), *Schizobasis* Baker (1873a: 105), *Tenicroa* Rafinesque (1837: 52), *Thuranthos* Wright (1916: 233) and *Urginea* Steinheil (1834: 321). On the other hand, Speta (1998a, 1998b, 2001) and Pfosser & Speta (2001) favoured a more refined approach, in which about 20 different genera were accepted. However, several of

these genera have been shown or interpreted to be para- or polyphyletic (Pfosser & Speta 2001, 2004, Manning *et al.* 2004, Pfosser *et al.* 2012). Similarly, contrasting taxonomic treatments were recently proposed in subfamily Ornithogaloideae (Speta 1998a, Manning *et al.* 2004, 2009, Martínez-Azorín *et al.* 2011). However, when sufficient plastid and nuclear DNA regions are included in the phylogenetic analyses, consistent morphological elements are fully congruent with clades, and these can be accepted at the generic rank, as shown by Martínez-Azorín *et al.* (2011). A similar taxonomic, morphologic and phylogenetic study in Urgineoideae combining four plastidial and one nuclear regions, covering 293 samples, ca. 160 species and 80% of total diversity in the subfamily is ongoing, that supports the recognition of a multigeneric treatment of the subfamily (Martínez-Azorín *et al.* submitted). Based on this evidence, some new genera have been recently described in Urgineoideae, viz. *Aulostemon* Martínez-Azorín *et al.* (2017: 288), *Austronea* Martínez-Azorín *et al.* (2018a: 105), *Iosanthus* Martínez-Azorín *et al.* (2019a: 584), *Mucinaea* Pinter *et al.* (2013: 296), *Sagittanthera* Mart.-Azorín, M.B.Crespo, A.P.Dold & Van Jaarsv. in Martínez-Azorín *et al.* (2013: 46), *Striatula* Pinter *et al.* (2019: 93), *Vera-duthiea* Speta (2016: 154) and *Zingela* Crouch *et al.* (2018: 36), given their distinct morphologies (Martínez-Azorín *et al.* 2013, 2017, 2018a, Pinter *et al.* 2013, 2019, Speta 2016, Crouch *et al.* 2018) and isolated positions in the phylogenetic trees (Martínez-Azorín *et al.* submitted).

Our field work in southern Africa during August 2016 resulted in the discovery of a remarkable new urgineoid species, found in gravelly soil at base of large south-facing cliffs on Pella se Berge, a distinctly elevated mountain situated in Northern Cape Province, South Africa (Fig. 1). The site is close to the Orange River and South Africa's northwestern border with Namibia. The new species shows a unique character in Hyacinthaceae, producing only three stamens associated with the inner tepal whorl, a feature that has in part informed the description of the new genus *Triandra*, at present monotypic. This solution is also supported by its phylogenetic relationships, as it constitutes an isolated lineage in Urgineoideae which is sister to the Madagascan endemic *Rhodocodon* (Martínez-Azorín *et al.* submitted), which shows very different morphology and a disjunct distribution. *Triandra pellabergensis sp. nov.* produces solitary hypogeal bulbs with compact scales, filiform proteranthous leaves, spurred bracts, lax racemes with few, nodding, nocturnal flowers with reflexed tepals, erect capsules with the withered tepals atop and flattened, winged seeds. The new species resembles *Urginea revoluta* Duthie (1928: 9) (*=Drimia hesperantha* Manning & Goldblatt 2003: 111) in general morphology, although the latter species consistently produces six stamens per flower, irregularly compressed, smaller seeds, and differs clearly in its phylogenetic relationships (Martínez-Azorín *et al.* submitted), ecology and biogeography. A complete morphological description is presented for the new genus and species, with discussion on its biology, ecology, distribution and phylogenetic relationships.

# Material and methods

Detailed morphological studies were undertaken on wild and cultivated specimens and herbarium material following the terminology used for species of Hyacinthaceae in Martínez-Azorín *et al.* (2007, 2009). Herbarium specimens from the herbaria ABH, BOL, GZU, GRA, K, NBG and PRE (acronyms according to Thiers 2021) were studied. Authors of the cited taxa follow IPNI (2021). Orthography of geographical names and grid-number system follows Leistner & Morris (1976).

# Results

Triandra Mart.-Azorín, M.B.Crespo, M.Á.Alonso, N.R.Crouch & M.Pinter gen. nov.

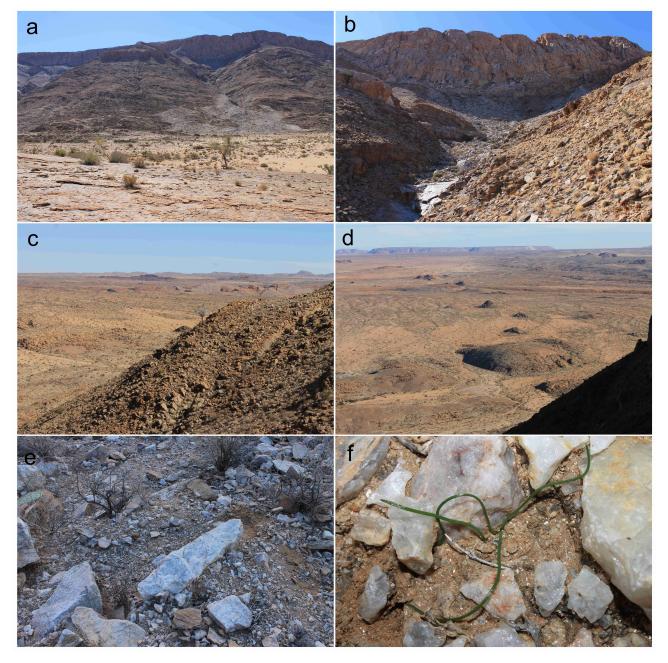
Typus generis: Triandra pellabergensis Mart.-Azorín, M.B.Crespo, M.Á.Alonso, N.R.Crouch & M.Pinter

*Diagnosis: Triandra* shows a unique combination of characters in Hyacinthaceae: filiform leaves; small, nodding, nocturnal flowers with three stamens; filiform, erect filaments; narrowly subclavate, erect style; erect capsule with withered perianth atop; and ellipsoid, flattened, winged seeds.

*Description*: Small bulbous geophyte. Bulb hypogeal, solitary. Leaves withered at flowering time, filiform, spreading and somewhat curved. Inflorescence a lax, elongate raceme, with few nodding, nocturnal flowers; bracts small, shorty spurred. Bracteoles absent. Tepals 6, biseriate, free or only very shortly connate at base, narrowly lanceolate, whitish with central longitudinal brown stripe on the abaxial side, strongly reflexed at full anthesis.

Stamens 3, associated with the inner tepal whorl; filaments filiform, white, erect and approaching the style at anthesis; anthers yellow, ovate, encircling the style, dehiscing longitudinally along their whole length, with yellow pollen. Ovary pale yellowish-green, ovoid, 3-locular, differentiated to the style. Style white, narrowly subclavate, erect, about as long as ovary. Stigma small. Capsule trilocular, loculicidal, ovoid to subglobose, erect, with remains of perigone circumscissile below and forming an apical cap, valves splitting to the base. Seeds black, flattened, distinctly winged with prominent embryo.

*Etymology*: The name of the new genus (greek; *Tri-*: three; *Andros, -a*: male) refers to the three stamens per flower.



**FIGURE 1.** Habitat of *Triandra pellabergensis* Mart.-Azorín *et al.* at the type locality, Pella se Berge, Northern Cape Province (South Africa). a–b. Pella se Berge and south facing cliffs. c–d. Views to the southwest from the type locality showing the desert habitat. e–f. Gravelly quartzitic soil among boulders at the type locality and plant in habitat at vegetative stage on 14 August 2016.

*Triandra pellabergensis* resembles *Urginea revoluta* in flower and leaf morphology, but the former species differs in consistently producing flowers with three stamens that are associated with the inner perianth whorl (not six, three also with the outer perianth whorl), and elliptical, flattened, winged seeds with a prominent embryo (not subpyramidal and irregularly compressed). *Triandra* occurs in the desert regions of northwestern South Africa, unlike *U. revoluta* which occurs in the fynbos vegetation of the southwestern Cape; phylogenetically, they represent distinct lineages.

**Type**:—SOUTH AFRICA. Northern Cape. Pofadder (2919): Pella, Pella se Berge, ca. 25 km W of Pofadder, rocky slopes at base of large south facing cliffs (–AA), 919 m elevation, among quartz and mica rocks, fl. ex hort. at University of Alicante on 29 June 2018, *M. Martínez-Azorín, M.B. Crespo, M.Á. Alonso et al. MMA1671b* (holotype: GRA; isotypes: ABH, K, PRE).

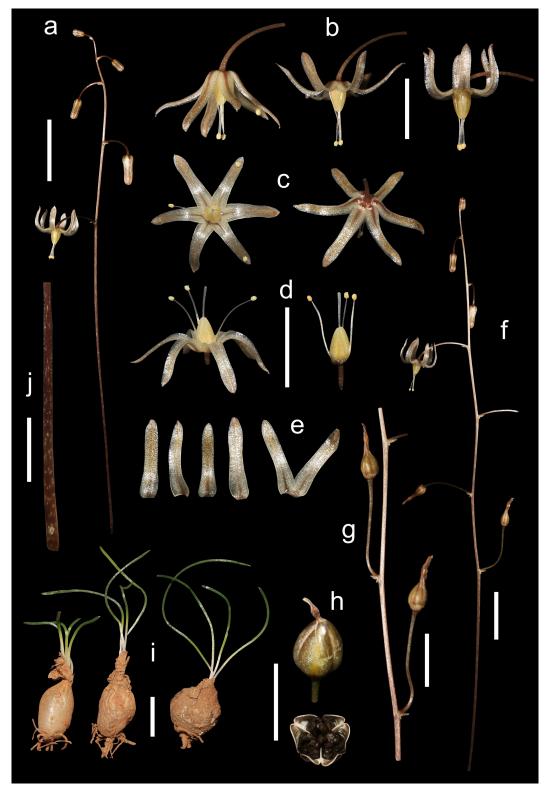
**Description**:—Small, herbaceous, deciduous geophyte. Bulb hypogeal, ovoid to subglobose,  $12-22 \times 8-18$ mm, depressed in old plants, solitary, with compact, white, thickened scales, and pale brown, membranous to papery outer tunics. Roots fleshy, white, branched,  $8-20 \times 0.5-1$  mm. Leaves 2–6, proteranthous and withered at flowering time, narrowly linear-filiform, hypogeal portion white, 2–10 mm long, aerial portion bright green,  $20-70 \times 0.8-1$ mm, spreading, somewhat curved-sinuous, slightly fleshy-succulent, subterete to slightly flattened, glabrous, smooth. Inflorescence an erect, lax raceme, 30-60 mm long, with 4-7, long pedicellate flowers; peduncle at anthesis 30-50 mm long, grevish to purplish-brown, erect, glabrous, smooth, with minute paler maculae at base; pedicels 12–15 mm long at anthesis, spreading and curving downwards, smooth; bracts small, ovate-lanceolate, 0.6–0.9 mm long, clasping the pedicels, the lowermost with a spur ca. 0.4 mm long. Flowers pentacyclic, trimerous, stellate, nodding, opening by dusk and withering before sunrise, 1-3 flowers open at a time, flower buds subcylindrical and somewhat constricted at the middle; tepals 6, entire, whitish with a brownish-green longitudinal central band on the abaxial side, slightly glandulous at the apex, biseriate, outer overlapping inner at the base, free or very shortly connate for 0.2 mm at base, spreading and strongly reflexed at full anthesis; tepals monomorphic,  $4.4-5.5 \times 1-1.2$  mm, narrowly lanceolate, slightly narrowed in the central portion, canaliculate. Stamens 3, free, opposite to the inner tepals whorl, erect and connivent to the style at full anthesis (initially spreading after bud opening – see Fig. 2b.c.d. left sides– but soon becoming erect and connivent to the style); filaments white, filiform, subterete, ca.  $4 \times 0.1$  mm, smooth; anthers yellow, ovate-oblong, ca. 0.3 mm long, dehiscing by longitudinal slits, with yellow pollen. Ovary pale yellow-green, ovate, truncate to the style, ca.  $2 \times 1.2$  mm; style white, narrowly subclavate, erect, ca.  $2.2 \times 0.1$  mm, subterete; stigma small, glandulose and minutely papillate. Capsule ovoid-globose, loculicidal,  $4-4.5 \times 3.5-4$  mm, valves splitting to the base, with the withered perigone segments circumscissile below and forming an apical cap. Seeds black, shining,  $2-2.7 \times 1-1.2$  mm, ellipsoid, flattened with prominent embryo and distinctly winged, testa surface reticulate, loose and easily detachable from the endosperm.

**Etymology**:—Named after the type locality of the species, Pella se Berge in the northwestern Northern Cape Province of South Africa close to the Orange River and the border with Namibia (Fig. 1). This mountain site is a type locality shared by two other remarkable Hyacinthaceae, *Bowiea gariepensis* van Jaarsveld (1983: 343) and *Eliokarmos craibii* Martínez-Azorín *et al.* (2015: 69).

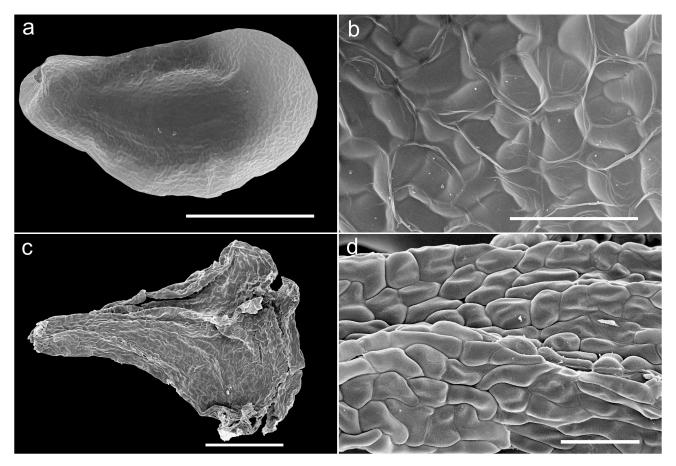
**Phenology**:—*Triandra pellabergensis* flowers from March to July in cultivation in the northern hemisphere and fruits appear from April to September. Leaves are proteranthous and completely withered at flowering time. Flowers are short-lived, opening by dusk and lasting few hours of a single night. In habitat, plants were in leaf in August (southern hemisphere Spring) at time of collection. Further studies are needed to evaluate its phenology in the wild.

**Habitat**:—This species is restricted to the Desert Biome and Eastern Gariep Rocky Desert (Dg 10) vegetation, growing in gravelly quartzitic soil among boulders, below south-facing large cliffs (Fig. 1) in positions that experience deep shade for most of the winter. The new species shares habitat with, among others, *Bowiea gariepensis*, *Tylecodon sulphureus* (Toelken 1977: 191) Toelken (1978: 381) subsp. *armianus* van Jaarsveld (1989: t. 1984) and *Whiteheadia bifolia* (Jacquin 1791: 215) Baker (1873b: 226). The region is characterized by annual precipitation ranging from 45 to 80 mm, peaking in late summer and early autumn, becoming more pronounced eastwards. Summer maximum temperatures often exceed 40°C, occasionally reaching 50°C at low elevations. Frost is very rare, but occurs at high elevations in the region (Mucina & Rutherford 2006) where the type locality is located.

**Distribution**:—*Triandra pellabergensis* is only known from the type locality, in Pella se Berge, Northern Cape Province of South Africa (Fig. 1). Further research is needed to evaluate its full extent of occurrence, whilst cognisant of its cryptic character.



**FIGURE 2.** *Triandra pellabergensis* Mart.-Azorín *et al.* from the type locality, Pella se Berge (South Africa), ex hort. at University of Alicante in March 2017. a. Inflorescence; b. Flowers in lateral view, showing different stages of tepal disposition; c. Flowers in frontal and dorsal views; d. Flower with spreading stamens (left) and fertile portion of flower (right), showing the diagnostic 3 stamens; e. Tepals; f. Inflorescence with immature capsules (one flower and part of its pedicel removed); g. Infructescence with erect capsules; h. Capsule with withered perianth cohering above, circumcissile below and forming an apical cap (above) and dehisced capsule showing seeds (below); i. Bulbs with leaves; j. Base of peduncle with slight maculation. Scale bars: a, f, i: 1 cm; b–e, g, h: 5 mm; j: 3 mm.



**FIGURE 3.** Seed morphology of *Triandra pellabergensis* Mart.-Azorín *et al.* (a–b) from the type locality, Pella se Berge (South Africa), and *Urginea revoluta* Baker (c–d) from *Esterhuysen 22771* (BOL): Scale bars: a: 1 mm; b, d: 100 µm; c: 500 µm.

**Diagnostic characters and taxonomic relationships**:—*Triandra pellabergensis* is identified by the solitary bulb; the 2–6 proteranthous, filiform, glabrous, leaves; the lax raceme with 4–7, pedicellate, nodding, nocturnal flowers; the reflexed tepals at anthesis; the 3, erect stamens associated with the inner tepal whorl; the erect and narrowly subclavate style; the erect capsules with the withered tepals atop; and the flattened, winged seeds with prominent embryo (Fig. 2, 3a–b). The new species is unique in Hyacinthaceae in having only 3 stamens per flower, with those associated with the outer tepal whorl being absent. Some genera with very specialized flowers in Hyacinthaceae, like those of *Albuca* Linnaeus (1762: 438) (subfam. Ornithogaloideae), sometimes lack anthers on the 3 outer stamens, due to the specialized pollination mechanism (Johnson *et al.* 2012), although their filaments, which are sometimes reduced, are always present. We have observed various plants of *Triandra pellabergensis* in cultivation during the past three years and all individuals and flowers consistently produced 3 stamens, and lacked the outer staminal whorl.

The nodding nocturnal flowers with reflexed tepals of *Triandra* superficially resemble those of other genera in Urgineoideae, such as *Thuranthos, Vera-duthiea* or some species of *Indurgia* Speta (2001: 169). However, the latter genera clearly differ in androecial, gynoecial and vegetative structures (cf. Crouch *et al.* 2018, Martínez-Azorín *et al.* 2018b, 2019b, Yadav *et al.* 2019). Our phylogenetic studies (Martínez-Azorín *et al.* submitted) have revealed that the latter three genera represent independent evolutionary lineages which present considerable convergence in flower morphology, adapted as they are to night pollinators. The above-mentioned phylogenetic study place a sample of *Triandra* as sister to the Madagascan endemic genus *Rhodocodon*, from which it can be readily separated on morphological grounds (cf. Knirsch *et al.* 2015, 2016, 2019); these molecular analyses further reveal *Triandra* to be distantly related to *Thuranthos, Vera-duthiea* and *Indurgia*.

In overall morphology, *Triandra pellabergensis* approaches *Urginea revoluta*, a similar-looking species that occurs in the coastal mountains of the southern Western Cape Province. However, this latter species produces larger bulbs (to 4 cm in diam.); fewer (1–2) leaves per bulb, each leaf to 25 cm long; a longer and flexuous raceme with more numerous (5–20) flowers; larger tepals (6–9 mm long), pedicels (10–15 mm long) which are reflexed in flower and articulated in their middle; six stamens per flower with longer filaments (ca. 5 mm long); subclavate style with

slightly capitate stigma; and notably angular, wrinkled seeds 2–2.5 mm long, with rugulose testa (Fig. 3c–d) (Duthie 1928, Manning & Goldblatt 2018). Manning & Goldblatt (2018) considered that Urginea revoluta is unique in the genus (Drimia, in their very broad sense covering nearly the whole subfamily Urgineoideae) in producing pedicels that abscise near the middle if the flowers are not pollinated, leaving a short, recurved basal portion 4–5 mm long attached to the scape, a character not observed in *Triandra*. There are also notable seed morphological differences between Triandra and U. revoluta, with those of the former being ellipsoidal, flattened and winged with a prominent embryo and reticulate testa (Fig. 3a-b), whilst in the latter they are subpyramidal, angular or irregularly compressed with a rugulose testa (Fig. 3c-d). We consider that the value of seed morphological characters has largely been understimated in the taxonomy and systematics of Urgineoideae. The current report well examples how two species that represent independent evolutionary lineages can show similar flower morphology (with covergence probably driven by nocturnal pollinators), and yet clearly differ in seed features (unconnected to pollination syndromes); both characters are widely used in other plant families to segregate genera. This is also evident when comparing angular or irregularly compressed seeds in genera such as *Litanthus* or *Geschollia* Speta (2001: 169), with those of genera (e.g. Urginavia, Thuranthos, Striatula, Vera-duthiea, etc.) that are better adapted to wind dispersal, being flattened and winged. Our unpublished phylogenetic analyses include a sample of U. revoluta from near Betty's Bay, Western Cape Province of South Africa, which resolves sister to a clade that includes Boosia macrocentra (Baker 1887: 702) Speta (2001: 169) and related taxa. The distinct genetic divergence between Urginea revoluta and Triandra (Martínez-Azorín et al. submitted) again indicates how the remarkable convergence of flower morphology may have been driven by nocturnal pollinators. To date, little work on pollinators of night-flowering urgineoids has been undertaken, but an extension of the work of Stirton (1976) should provide insights into the character of evolutionary processes that have led to the observed floral form convergence.

In summary, *Triandra pellabergensis* shows a unique syndrome of morphological characters within Urgineoideae, representing an independent evolutionary lineage for which a new genus is accordingly described.

# Additional material studied:

*Triandra pellabergensis* (paratypes):—SOUTH AFRICA. Northern Cape. Pofadder (2919): Pella, Pella se Berge, ca. 25 km W of Pofadder, rocky slopes at base of large south facing cliffs (-AA), 919 m elevation, 14 August 2016 (vegetative), among quartz and mica rocks, *M. Martínez-Azorín, M.B. Crespo, M.Á. Alonso et al. MMA1671* (ABH 74374!).

Urginea revoluta:-SOUTH AFRICA. Western Cape. Worcester (3319): Worcester Division, Bailey's Peak, Bains Kloof, mts. stony E. slopes (-CA), 3000 feet elevation, after fire, 21 February 1954 (in fruit), E. Esterhuysen 22750 (BOL!); Worcester (3319): Paarl Division, Zuurvlakte, above Du Toitskloof, head of Pass (-CA), 3000 feet elevation, on stony plateau, after fire, 27 February 1954 (in fruit), E. Esterhuysen 22771 (BOL!); ibidem, grown at B.H., bulbs passed 15 November 1954, 7 March 1954 (in fruit), E. Esterhuysen 22771 (BOL!); Simonstown (3418): Stellenbosch Division, burnt stony slope above Diepgat, Somerset West (-BB), 1500-2000 feet elevation, 8 January 1950 (in flower), E. Esterhuysen 16727 (BOL!); Simonstown (3418): Fairy Glen, Palmiet River mouth (-BD), 450 feet elevation, 7 December 1896 (in flower), H. Bolus s.n. (BOL!); Simonstown (3418): Caledon Division, mts. near Palmiet River mouth, lower south slopes (-BD), 25 January 1947 (in flower), E. Esterhuysen 13672 (BOL! two sheets); Simonstown (3418): Caledon Division, Palmiet River (-BD), in rock crevices on river bank, 29 December 1941 (in flower), F.M. Leighton sub BOL22719 (BOL!, NBG!); Simonstown (3418): Kogelberg Reserve, Oudebos, across Palmiet River (-BD), rocky soil, sand, fynbos, recently burned, 6 January 2001 (in flower), J.C. Manning 2303 (NBG!, 2 sheets); Simonstown (3418): Simostown, Kogelberg State Forest, Dwars River Mountain, foothills near Somersfontein (-BD), ca. 300 m elevation, dry flat coarse sandy soil, burnt September 1971, 12 January 1973 (in flower), C. Boucher 2063 (PRE barcode 0734884!); Simonstown (3418): Kogelberg S.F., Kogelberg Research Site, burnt plot KBE3 (-BD), ca. 120 m elevation, washed out TMS, deep soil, 16 March 1977, B.J. Durand 189 (PRE barcode 0813763!); Simonstown (3418); Caledon Division, mt. slopes at Rooi Els (-BD), 5 February 1947 (in flower), E. Esterhuysen 13714 (BOL!); Caledon (3419): circa Elim, district Bredasdorp (-DA or -DB), ca. 20 m elevation, coarse sandy soil on 15° slope, area burnt September 1971, 8 January 1972 (in flower), C. Boucher 1776 (BOL!, PRE barcode 0240617!); Caledon (3419): Caledon Division, Riviersonderend Mts., slopes near R. Z. E. village, after fire, 20 November 1955 (in flower and fruit), E. Esterhuysen 25329 (BOL!); Caledon (3419): Fernkloof Nature Reserve, Hermanus (-AD) (Photo! https://www.fernkloof.org.za/index.php/all-plants/plant-families/item/drimia-hesperantha); Caledon (3419): Hemel & Aarde Valley, Hermanus, Overberg District Municipality (-AD), -34.389903 S 19.255905 E, 14 February 2020, D. Marais (photos! https://www.inaturalist.org/observations/38629796); Caledon (3419): Phillipskop Mountain Reserve (-AD), -34.40353 S 19.5319978 E, 8 March 2019, *C. Whitehouse* (Photos! https://www. inaturalist.org/observations/21261605); Caledon (3419): Sandberg Fynbos Reserve (-DA), -34.599068 S 19.678738 E, 17 January 2019, *J. Deacon* (Photos! https://www.inaturalist.org/observations/19825761); Bredasdorp (3420): De Hoop, near turn off from Potberg road (-AD), foot of limestone hills, 6 February 1998 (in flower), *P. Goldblatt & J.C. Manning 10857* (NBG!, MO).

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