A revision of Tecophilaeaceae subfam. Tecophilaeoideae in Africa

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ABSTRACT

Family Tecophilaeaceae subfam. Tecophilaeoideae is revised for the Flora of southern Africa region, with the inclusion of the tropical Walleria mackenzii J.Kirk for completeness. The genera Cyanella Royen ex L. (9 spp.), Eremiolirion J.C.Manning & F.Forest (1 sp.) and Walleria J.Kirk (3 spp.) are treated, with keys to the genera, species and subspecies; and full descriptions and distribution maps. A formal infrageneric classification is proposed for Cyanella, in which sect. Trigella (Salisb.) Pax & K.Hoffm. is revised for the species with a 3 + 3 arrangement of stamens. The new species, C. marlothii J.C.Manning & Goldblatt, is described from the Richtersveld; and C. pentheri Zahlbr. is resurrected from the synonymy of C. hyacinthoides Royen ex L. Pink-flowered plants of normally yellow-flowered C. lutea have a separate geographical distribution and are recognized as subspp. rosea (Eckl. ex Baker) J.C.Manning & Goldblatt.

INTRODUCTION

Tecophilaeaceae is a small family of seven or eight genera and ± 25 species from California, Chile, and southern and tropical mainland Africa (Simpson & Rudall 1998). The reported occurrence of the family in Madagascar (Simpson & Rudall 1998) is based on Walleria paniculata Fritsch, a synonym of Dianella ensifolia (L.) DC. (Hemerochilaceae). The family is best represented in Africa, where almost two thirds of the species are found. Cynastrum Oliv. (3 spp.) and Kabuyea Brummitt (1 sp.) are strictly tropical, but Walleria J.Kirk (3 spp.), Eremiolirion J.C.Manning & F.Forest (1 sp.), and Cyanella Royen ex L. (9 spp.), are primarily distributed in subtropical and temperate southern Africa. Members of the family are perennial herbs with a cormous, usually tufted rootstock, basal (rarely caulescent) leaves, and long-lasting flowers, typically in racemose or paniculate, cymose inflorescences; but sometimes solitary and axillary. The flowers are actinomorphic or zygomorphic, with 3 + 3 petaloid tepals fused into a short tube adnate to the ovary, and six stamens, all fertile or some reduced to staminodes, with ± porose dehiscence. The ovary is inferior or semi-inferior and 3-carpellate, and matures into a loculicidal capsule (Simpson & Rudall 1998; Heywood et al. 2007).

The two tropical African genera, Cynastrum and Kabuyea, have been the subject of a detailed review (Brummitt et al. 1998), in which they were segregated as subfam. Cynastridorae, with the remaining genera of the family retained in subfam. Tecophilaeoideae. The taxonomy of the southern African species is relatively well understood, and both Cyanella and Walleria were revised fairly recently (Carter 1962; Scott 1991; Cowley & Brummitt 2001), including historical and morphological details. Since then, however, the genus Eremiolirion has been established to accommodate Cyanella amboensis Schinz, which was excluded from Cyanella by Scott (1991), but unplaced. We have also published additional observations on the distribution and morphology of Walleria gracilis (Salisb.) S.Carter (Manning et al. 2001). It is now clear that there is more variation in some species of Cyanella than was recognized by Scott (1991), and three subspecies have since been described in C. alba L.f. (Manning et al. 2005). Field study and examination of herbarium material of C. hyacinthoides Royen ex L. suggest that this species is currently too broadly circumscribed, and that C. pentheri Zahlbr. should be resuscitated from synonymy. In addition, the clear geographical segregation between the typical yellow-flowered and the pink-flowered forms of C. lutea L.f. is appropriately reflected by the recognition of distinct subspecies for them. A collection from the Richtersveld, until now identified as C. orchidiformis Jacc., differs from that species and from all others in the genus in having all six filaments connate into a staminal tube. It evidently represents an unnamed species that we describe here.

Currently, therefore, there is no comprehensive treatment for the family in southern Africa and the available treatment of Cyanella is inadequate and incomplete in some respects. We provide here a complete review of the genera and species occurring in the Flora of southern Africa region, including also the tropical African Walleria mackenzii J.Kirk for completeness. We also propose a new infrageneric classification for Cyanella that associates morphologically similar species in two sections, with the larger of the two, sect. Cyanella, subdivided into two series.

MATERIALS AND METHODS

Type specimens or digital images of types from the relevant herbaria were examined for all names, as well as all available herbarium specimens in BOL, NBG, PRE, and SAM (herbarium acronyms after Holmgren et al. 1990). Particular use was made of high-resolution digital images on the Aluka website (www.aluka.org), and of the Herbarium of the Linnean Society of London (www.linnean-online.org).
**TAXONOMY**

**Key to genera**

1a Corm not tunicated; leaves cauline; flowers solitary in leaf axils; seeds verrucose or papillate, with tufts of trichomes, brown ........................................... Walleria

1b Corm with fibrous tunics; leaves racemose or paniculate cymes; seeds rugose, glabrous, black:

2a Foliage leaves 2; inflorescence a divaricate panicle; pedicels without a bracteole; flowers actinomorphic; stamens monomorphic, central, and symmetrical .................................. Eremioridion

2b Foliage leaves 1; inflorescence a raceme, usually branched, rarely condensed and flowers apparently solitary; pedicels bracteolate; flowers zygomorphic; stamens dimorphic, in two groups of 3 + 3 or 5 + 1 ................. Cyanella


**Androsyne Salisb:** 61 (1866). Type species: A. gracilis Salisb. = Walleria gracilis (Salisb.) S.Carter.

Deciduous geophytes with deep-seated, non-tunicated corm; subterranean portion of stem developing paired adventitious roots at each node, aerial portion of stem erect or straggling, smooth, scabrid or armed with recurved prickles. *Cataphylls* numerous, scattered along subterranean portion of stem, small, tubular, membranous. Foliage leaves numerous, all cauline, alternate, sessile or amphipectal, linear to ovate, acute or cirrhose and tendriliferous, midrib sometimes armed with recurved prickles beneath. *Inflorescence* of solitary, axillary flowers, or rarely bracteole subtending a second flower; pedicels erect or cormeous, smooth or prickly, with solitary bracteole inserted ± midway. *Flowers* actinomorphic, erect or nodding, rotate, white to blue; tepals connate below into short tube, ± similar. *Stamens* 6, monomorphic, erect-symmetrical, inserted at mouth of tube; filaments short; anthers basifixed, erect, free, or connivent around style, narrowly lanceolate, dehiscing by apical pores, outer surface scabridulous in basal 1/2. *Ovary* ± superior, with several ovules per locule; style terete, erect, filiform. *Capsules* ovoid to subglobose. *Seeds* ovoid, brown, surface warty or produced into finger-like papillae, each with apical tuft of minute trichomes. *Basic chromosome number:* x = 12 (Goldblatt & Manning 1989).

3 spp., southern and southern tropical Africa.

**Etymology:** the genus is named for Horace Waller, who made the first collections of both tropical African species during an expedition to central Africa in 1863.

**Ethnobotany:** the corms comprise part of the traditional diet of the San, Tswana, and other indigenous tribes (e.g., Leffers 2008; also Llagard 289, Maguire 2194, Nysman & Nolles 231, Story 6117).

**Key to species**

1a Flowers erect, tepals 13–22 mm long; anthers free, not connivent, blue, purple, or black with yellow base and apex, 6–12 mm long; style 8–15 mm long .................. 1. *W. mackenzii*

1b Flowers nodding, tepals 6–16 mm long; anthers connate and connivent, yellow at least in basal 1/2, 4–8 mm long; style 4.0–8.5 mm long:

2a Plants erect or sprawling, free-standing, mostly unbranched; stems and pedicels smooth, scabrid or with hooked prickles; leaves not cirrhose; tepals plain white, pink, mauve, or blue ........................................... 2. *W. nutans*

2b Plants usually straggling or climbing, well branched; stems and pedicels always armed with hooked prickles; upper leaves cirrhose, with tendril-like apex; tepals white with basal purple blotch ........................................ 3. *W. gracilis*


Deciduous geophyte, 180–900 mm high. *Corm* subglobose or depressed-globose, 20–40 mm diam. *Stem* erect, mostly simple or with 1 or 2 branches, smooth or rarely scabrid or minutely prickly. *Leaves* ovate to narrowly lanceolate, 30–110 × (4–)5–20–(28) mm, upper narrower, base cuneate or weakly cordate but not amplexicaul, apex acute or rarely cirrhose, midrib smooth, sometimes scabrid or minutely prickly. *Flow- ers* solitary in axils in central portion of stem, erect, sometimes with additional flower developed in axil of bracteole; pedicels ascending and ± erect at flowering, straight or flexible, becoming deflexed or pendulous in fruit, 13–60 mm long, smooth or scabrid, with lanceolate bracteole 10–26 mm long inserted ± halfway, rarely lacking; tepals white, pink, or mauve to pale or bright blue, spreading, elliptic–lanceolate, 13–22 × 2.5–6.5 mm, inner slightly narrower than outer. *Stamens* erect, free and not connivent; filaments 1–3 mm long, awl-shaped; anthers 6–12 mm long, blue to purple or black with yellow base and apex, pores circular, apical. *Ovary* subglobose-pyramidal, 3-lobed above, ± 3 mm long; style 8–15 mm long. *Capsule* subglobose or ovoid, 10–20 mm long, maturing to dark yellow. *Seeds* ovoid, ± 5 mm long, dark mahogany-brown, papillate, papillae becoming longer and more finger-like in distal half, each with apical tuft of minute trichomes. *Flowering time:* mainly Nov.–Jan.(–Mar.), shortly after the onset of the rains.

**Distribution and ecology:** distributed across southern tropical Africa, from the higher-lying parts of central Angola, Zambia, and southern Democratic Republic of Congo, through Malawi into southern and western Tanzania [see Carter (1962) for map]. The species is largely restricted to higher rainfall areas, where it occurs in open woodland and savanna, often in rocky outcrops.

**Diagnosis and relationships:** distinguished from other species of Walleria by its generally more robust habit, erect, mostly larger flowers with tepals 13–22 mm long, and free anthers not cohering at the tips, predominantly blue to purple or black with only the base and tips yellow, and dehiscing through terminal, circular pores. *Walleria mackenzii* is likely to be confused only with *W. nutans*, which has nodding flowers with tepals 6–16 mm long and connivent anthers, connate at the tips, and dehiscing through short, subapical, intorse slits.


*W. hockii* De Wild.: 8 (1915). Type: Northern Rhodesia [Zambia], Kafue Valley, 1911, *A. Hock* s.n. BR8642639 (BR, holo.).

Deciduous geophyte (70–)100–300 mm high. Corm subglobose or depressed-globose, 20–30 mm diam. Stem erect or sprawling but never climbing, mostly simple or with 1 or 2 branches, rarely more, smooth or variously prickly with delicate, recurved prickles 0.5–1.5 mm long. Leaves linear to narrowly lanceolate, (30–)70–150 × (2–)5–7(–12) mm, upper narrower and attenuate, base cuneate or weakly cordate but not amplexicaul, midrib smooth or with recurved prickles beneath. Flowers solitary in axils in central portion of stem, nodding, sometimes with additional flower developed in axil of bracteole; pedicels suberect but sharply decurved distally, 20–50(–80) mm long, smooth or scabrid, with lanceolate bracteole 10–15 mm long inserted in upper third or quarter; tepals white, pink, or mauve to pale blue, recurved or reflexed, bracteole, (6–)10–16 × 2–5 mm. Stamens connivent, connate at tips; filaments 0.5–1.0 mm long; anthers (4–)6–8 mm long, mostly yellow with narrow purple band across distal third and with grey tips, slits short, subapical, introrse. Ovary subglobose-pyramidal, 3-lobed above, ± 3 mm long; style 5.0–8.5 mm long. Capsule ovoid, shortly apiculate and 3-lobed above, 8–17 mm long, green, yellow or orange. Seeds ovoid, ± 5 mm long, dark mahogany-brown, papillate, papilae becoming longer and more finger-like in distal half, each with apical tuft of minute trichomes. Chromosome number: 2n = 12 (Goldblatt & Manning 1989). Flowering time: Nov.–Jan. (–Mar.). Figure 1A, B.

Distribution and ecology: widely distributed through subtropical Africa, from the higher-lying parts of central and northern Namibia and southern Angola through Zambia into eastern Botswana and the northern part of South Africa, where it has been recorded from the Soutpansberg into central Limpopo, adjacent Mpumalanga and North West Province, and southwest as far as Taung in Northern Cape (Figure 2). Plants occur in open savanna, mostly in sandy soils but also on limestone flats and dolomite rock sheets.

Diagnosis and relationships: closely resembling the southwestern Cape *W. gracilis*, with which it shares nodding flowers with apically connivent anthers dehiscing through introrse, subapical pores and sometimes prickly stems, pedicels, and abaxial leaf midribs. *Walleria nutans* is distinguished by its free-standing, mostly

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unbranched stems, leaves without tendrill-like tips, and unmarked, white, pink, or mauve to pale blue tepals. The stems, pedicels and underside of the leaf midribs may be smooth or variously armed with recurved prickles, but these are delicate, almost bristle-like, and mostly < 1 mm long, and the anthers are mostly yellow, with the purple and grey banding restricted to the apical third. The presentation of the flowers is subtly different in the two species: pedicels in \textit{W. nutans} are essentially suberect up to the level of insertion of the bracteole in the upper third or quarter, at which point the pedicels are sharply decurved, whereas the bracteoles in \textit{W. gracilis} are mostly inserted ± midway along the pedicels, which are therefore more arcuate.

**Vernacular name:** bush potato.

**Representative specimens**


\textbf{BOTSWANA.—2225 (Mokatini): N of Lephede, 100 km W of Serowe, (–BC), Feb. 1982 (fruiting), Smynan & Noailles 231 (PRE). 2426 (Mochudi): Mochudi, (–AC), without date, Rogers 6739 (BOL).}


\textbf{MPUMALANGA.—2430 (Pilgrim’s Rest): Nootigedacht mtn, near Branddraai, (–DA), 24 Nov. 1933, Young 4688 (BOL, PRE).}

\textbf{NORTHERN CAPE.—2724 (Taung): Barkly West, Madipelessa, (–CA), 26 Feb. 1937, Acocks 1822 (PRE).}


\textit{W. armata} Schltr. & K.Krause in Krause: 235 (1921). Type: South Africa, [Western Cape, near Klawer], [Farm] Windhoek, 8 July 1896, R. Schlechter 8074 (B, holo. [not seen]; BM!, BR!, CO!, GRA!, K, MO!, PRE!, S!, iso.). [The collection was published as Schlechter 2074 in the protologue, evidently a misprint].

Deciduous geophyte, 100–700 mm high. \textit{Corm} subglobose or depressed-globose, 20–30 mm diam. Stem straggling or climbing, well branched, with recurved prickles 1.0–1.5 mm long in upper parts. \textit{Leaves} lanceolate to narrowly lanceolate, (30–)70–120 × 5–10 mm, upper narrower and attenuate-cirrhose, apex coiling and tendril-like, amplexicaul, midrib with recurved prickles beneath. \textit{Flowers} solitary in axils in central portion of stem, nodding, rose-scented; pedicels arcuate, 20–40 mm long, sparsely prickly, with lanceolate bracteole 6–10 mm long inserted ± midway; tepals white with purple blotch at base, recurved or reflexed, lanceolate, 10–16 × 2.5–3.5 mm. \textit{Stamens} connivent, connate at tips; filaments 0.5–1.0 mm long; anthers 5–6 mm long, yellow in lower 1/2 and purple above with grey tips, slits short, subapical, introrse. \textit{Ovary} subglobose-pyramidal, 3-lobed above, ± 2 mm long; style ± 4 mm long. \textit{Capsule} ovoid, ± 15 mm long, shortly apiculate and 3-lobed above. \textit{Seeds} ovoid, ± 5 mm long, dark mahogany-brown, with conspicuous apical cluster of finger-like papillae, each topped with tuft of minute trichomes, rest of seed ± smooth but covered with trichome-tufts. \textit{Flowering time}: June and July. Figure 1C–K.

**Distribution and ecology:** The species has a limited, curiously scattered distribution along the west coast of South Africa. It is best known from the lower reaches of the Olifants River in Western Cape, where it has been recorded along the foot of the Gifberg east of Klawer and on Pakhuis Pass, some 50 km to the south (Figure 3). At these localities, the species occurs in deep sand among outcrops of Cape sandstone in arid fynbos vegetation. There is evidently a large disjunction in the distribution, based on a single enigmatic collection made by Rudolph Marloth in 1925 from near Kuboes in the Richtersveld. This locality, 60 km upstream from the mouth of the Orange River, is 350 km north of Klawer, and to date \textit{W. gracilis} has not been re-collected there; nor from the intervening country. Although the identity of the Kuboes collection is not in doubt, it is unfortunately a plant that was cultivated to flowering in Cape Town five years later; and although the label is explicit in identifying the location at which the tuber was originally collected, the possibility that the locality has been confused must be considered until the species is rediscovered in the Richtersveld.

Plants may reach up to 600 mm in height when supported by small shrubs, but are much shorter in the open. The nodding, \textit{Solanum}-like flowers are evidently adapted to buzz pollination, probably by solitary bees in the family Apidae: Anthophorinae (Manning et al. 2001).
Diagnosis and relationships: the species closely resembles *W. nutans* from subtropical Africa and was treated as conspecific with it by Phillips (1951), but the two are quite distinct. *Walleria gracilis* is recognized by its straggling or climbing habit, well-branched stem, more robust prickles ± 1.0–1.5 mm long, upper leaves by its straggling or climbing habit, well-branched stem, and apical pores. Around style, narrowly lanceolate, dehiscing by oblong filaments short; anthers basifixed, erect and connivent phic, erect-symmetrical, inserted near mouth of tube; ovary half-inferior, with several ovules per locule; style terete, erect, filiform. Capsules ovoid to globose. Seeds ellipsoid-pyriform, blackish brown, testa surface rugose.

Additional specimens seen


Deciduous geophyte with deep-seated, tunicated corm, tunics decaying into firm-leathery, coarsely netted fibres extending into neck 10–60 mm long, pale whitish brown. Leaves 2, basal, suberect, narrowly lanceolate, (10–)15–25 × (8–)10–20 mm, attenuate, canaliculate with prominent midrib abaxially, leathery. Inflorescence a divaricately branching, paniculate cyme with (1–)3–7-branches, up to 30-flowered; pedicels cernuous at tip, 15–25 mm long, elongating slightly in fruit and straightening, ultimately 20–40 mm long. Flowers nodding, campanulate, white flushed pink or maroon abaxially at base of outer tepals, fragrant; perianth tube ± 4 mm long, with fringed corona 0.5–1.0 mm high at mouth of tube forming collar extending over ovary to surround base of style; outer tepals spreading from base, oblong, 15–20 × 5–7 mm, obtuse, margins revolute, inner tepals at first suberect but spreading in upper 1/2, pandurate and short-clawed, claw ± 2 mm long, blade ovate, 13–18 × 7–10 mm, apex slightly cucullate, margins crisped. Stamens monomorphic; filaments terete, ± 0.25 mm; anthers narrowly lanceolate, 9–10 mm long, yellow, dehiscing by oblong apical pores 1.5 mm long. Ovary half-inferior; ovules ± 6 per locule; style 10–12 mm long, extending shortly beyond anthers, white. Capsules ovoid to globose, 10–12 × 8–12 mm. Seeds ellipsoid-pyriform, 4.0–4.5 × 3.0–3.5 mm, blackish brown; testa surface rugose. Flowering time: (mid-Jan.–)Feb.–Mar.–(early Apr.). Figure 4.

**Eremiolirion amboense** (Schinz) J.C.Manning & C.A.Mannheimer in Bothalia 35: 117 (2005). Type: South West Africa [Namibia], Amboland [Ovamboland], Ondonga, [Ondongwa], without date, Rautanen 344 (Z, holo.).

Plants (60–)100–250 mm high. Corms deep-seated, 30 mm diam; tunics decaying into firm-leathery, coarsely netted fibres extending into neck 10–60 mm long, pale whitish brown. Leaves 2, basal, suberect, narrowly lanceolate, (10–)15–25 × (8–)10–20 mm, attenuate, canaliculate with prominent midrib abaxially, leathery. Inflorescence a divaricately branching, paniculate cyme with (1–)3–7-branches, up to 30-flowered; pedicels cernuous at tip, 15–25 mm long, elongating slightly in fruit and straightening, ultimately 20–40 mm long. Flowers nodding, campanulate, white flushed pink or maroon abaxially at base of outer tepals, fragrant; perianth tube ± 4 mm long, with fringed corona 0.5–1.0 mm high at mouth of tube forming collar extending over ovary to surround base of style; outer tepals spreading from base, oblong, 15–20 × 5–7 mm, obtuse, margins revolute, inner tepals at first suberect but spreading in upper 1/2, pandurate and short-clawed, claw ± 2 mm long, blade ovate, 13–18 × 7–10 mm, apex slightly cucullate, margins crisped. Stamens monomorphic; filaments terete, ± 0.25 mm; anthers narrowly lanceolate, 9–10 mm long, yellow, dehiscing by oblong apical pores 1.5 mm long. Ovary half-inferior; ovules ± 6 per locule; style 10–12 mm long, extending shortly beyond anthers, white. Capsules ovoid to globose, 10–12 × 8–12 mm. Seeds ellipsoid-pyriform, 4.0–4.5 × 3.0–3.5 mm, blackish brown; testa surface rugose. Flowering time: (mid-Jan.–)Feb.–Mar.–(early Apr.). Figure 4.

Distribution and ecology: locally common through the higher-lying parts of west-central and southwestern Namibia, occurring along the better watered, western edge of the escarpment from west of Mariental in the south to Kaokoland in the north (Figure 5) and in southwestern Angola near Lake Arco. The species typically occurs in colonies, often numbering many individuals, in sandy loam or heavy clay soils, especially in stony or gravelly situations. Flowering is dependent on rainfall.

The flowers close at night ± 21:00, re-opening in the morning ± 09:00. They are fragrant during the day, with a jasmine-like fragrance at first but later smelling of stale urine, and are visited by bees and the occasional moth (*Ward, Ward & Ward 10518*).

Vernacular name: desert snowdrop.

Representative specimens

FIGURE 4.—Eremiolirion amboense: A, flowering plant; B, flower; C, inner tepal; D, outer tepal; E, half-flower; F, androecium with style; G, capsule; H, seed. Scale bar: A–D, G, 10 mm; E, F & H, 2 mm. Artist: John Manning.

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(Khorixas): S side of watershed Ugb/Huab Rivers W of Brandberg, (–CA), 10 Feb. 1966; Giess 9131 (PRE, WIND); Farm Greylinghof SW 107, (–BD), 16 Feb. 1963; Giess, Volk & Bleitersor 5158 (PRE, WIND).

**Cyaneella Royen ex L., Genera plantarum, edn. 5: 149 (1754).** Type species: *Cyaneella hyacinthoides* Royen ex L.


**Note:** Pax & Hoffmann (1930) inadvertently transposed the species and diagnoses of their sections Pharetrella and Trigella, assigning *Cyaneella alba* to sect. Trigella and *C. orchidiformis* to sect. Pharetrella, thus precisely opposed to Salisbury’s (1866) original placement. As Pax & Hoffmann were explicitly making combinations based on Salisbury’s genera, however, the types are fixed according to Salisbury’s designations, which are followed here.

Deciduous geophytes with deep-seated, tunicated corm, tunics decaying into fibrous or firm-leathery, coarsely netted fibres, sometimes extending into neck. *Cataphyll* 1, extending to ground level and enclosing leaf sheaths, entirely sheathing or with short leafy blade. Stem simple or branched, smooth or minutely and sparsely scabridulous. *Foliage leaves* 3–12, basal, lanceolate to linear-lanceolate and canaliculate or filiform-terete, firm-textured or softer, margins plane, undulate or crispulate, smooth or scabridulous or ciliate, sur-

face mostly glabrous, rarely puberulous. **Inflorescence** a raceme, usually branched, rarely highly condensed and flowers apparently solitary, with bracts subtending branches and pedicels; pedicels suberect or spreading, with solitary bracteole inserted ± midway. **Flowers** zygomorphic (perianth only weakly so through tepal orientation) or asymmetric (enantiomorphic) through stylar flexure, spreading-rotate, white, yellow, orange, pink, or mauve to blue, sometimes distinctly veined or patterned, scented; tepals free, spreading or reflexed, ± similar or weakly dimorphic with inner broader, ovate to oblancoelate, lower concave or ± cucullate. **Stamens** 6, dimorphic, either with 3 smaller posterior stamens plus 3 larger anterior stamens, or 5 smaller posterior stamens plus 1 larger anterior stamen and then lowermost either median or flexed laterally to left or right, suberect, upper stamens arcuate, lower stamen(s) declinate; filaments stout; anthers basifixied, upper sometimes adherent, narrowly lanceolate, dehiscing by apical pores or short, introrse slits. **Ovary** half-inferior, with several ovules per locule; style terete, declinate, filiform, median or flexed opposite lower stamen in enantiomorphic species. **Capsules** ovoid to globose. **Seeds** ovoid, black, or dark brown, testa surface rugose or scalariform. **Basic chromosome number:** $x = 12$ (Ornduff 1979).

9 spp., southern Namibia and southwestern South Africa, mainly winter rainfall parts.

**Etymology:** the name is a compound of the Greek *kyanus* (blue) and -*ella* (diminutive), alluding to the small blue flowers of *Cyaneella hyacinthoides*, the first species to be described.

**Etnobotany:** the corms comprise part of the traditional diet of the Nama tribes (*Archer 410*).

I. Section **Trigella** (Salisb.) Pax & K.Hoffm. in Die natürlichen Pflanzenfamilien 15a: 427 (1930). **Trigella**

Key to species

1a Stamens 3 + 3; flowers pink or mauve (sect. *Trigella*):

2a Leaves linear, occasionally narrowly lanceolate, 2–8 mm wide; perianth not patterned; capsules subglobose-ovoid, 6–10 mm long; plants from southern Namibia and Richtersveld:

3a Tepals 10–12 mm long; filaments connate < halfway into short tube ± 1 mm long; anthers yellow throughout; style 10–15 mm long, ± twice as long as lower stamens

4b Tepals 8–10 mm long; posterior (upper) filaments arcuate or geniculate-sigmoid, ± evenly thick throughout, not flexuous distally; anterior (lower) anthers 2.5–3.0 mm long

5b Tepals 13–20 mm long; filaments connate halfway or more into tube 1–2 mm long; anthers greyish or mauve distally; style ± 6 mm long, only slightly longer than lower stamens

6b Raceme congested, flowers apparently solitary among leaves; pedicels 80–120 mm long

7b Raceme dense, lower flowers 0.5–0.6 × their length apart; bracteoles sub-basal; perianth orange

8a Upper cataphyll purple-reticulate; leaves linear, mostly 1–4 mm wide, margins conspicuously ciliate in basal half with long, shaggy cilia 2–3 mm long but ± smooth distally

9a Raceme lax, lower flowers 1.5–3.0 × their length apart; bracteoles sub-basal; perianth orange

7a Raceme lax, lower flowers 1.5–3.0 × their length apart; bracteoles sub-basal; perianth orange

8b Upper cataphyll usually pale, rarely purple-reticulate; leaves linear or lanceolate, mostly 4–15 mm wide, margins smooth or ciliolate along entire length with short hairs up to 1 mm long

1a Stamens 5 + 1; flowers white, yellow, orange, pink, or mauve to blue (sect. *Cyaneella*):

5a Pedicels suberect; filaments connate at base only; style laterally deflexed to left or right opposite lower stamen and flowers enantiomorphic:

6a Raceme not congested; pedicels 15–30 mm long

7a Raceme lax, lower flowers 1.5–3.0 × their length apart; bracteoles sub-basal; perianth orange

8b Raceme congested, flowers apparently solitary among leaves; pedicels 80–120 mm long

9b Raceme congested, flowers apparently solitary among leaves; pedicels 80–120 mm long

10b Raceme congested, flowers apparently solitary among leaves; pedicels 80–120 mm long

11b Raceme congested, flowers apparently solitary among leaves; pedicels 80–120 mm long

12b Raceme congested, flowers apparently solitary among leaves; pedicels 80–120 mm long

13b Raceme congested, flowers apparently solitary among leaves; pedicels 80–120 mm long

14b Raceme congested, flowers apparently solitary among leaves; pedicels 80–120 mm long

15b Raceme congested, flowers apparently solitary among leaves; pedicels 80–120 mm long

16b Raceme congested, flowers apparently solitary among leaves; pedicels 80–120 mm long
Salisb.: 46 (1866). Type species: *Cyanella orchidiformis* Jacq.

*Flowers* never enantiostylyous; perianth pink to mauve, sometimes patterned. *Stamens* 3 + 3, lower anthers tapering, upper anthers ± sagittate. *Ovary*: style median.


*C. krauseana* Dinter & G.M.Schulze: 525 (1941). Type: Namibia, Klinghardtsgiebige, 23 Sept. 1922, M.K. Dinter 3955 (B, holo.†; PRE!, SAM!, iso.).

Plants 80–200 mm high. *Corms* moderately or very deep-seated, 15–30 mm diam., tunics of coarsely netted, wiry fibres, extending shortly into a fibrous neck to 20 mm long, pale brown or grey. *Basal leaves* 4–6, spreading or suberect, linear to narrowly lanceolate, 50–150(–200) × 2–8 mm, acute to attenuate, plane, spreading or suberect, linear to narrowly lanceolate, ± 3–5 mm long, yellow, anthers ± sagittate, outer smaller, ± 1.5 mm long, yellow; filaments of anterior cluster deflexed, 2.0–2.5 mm long, shortly connate for half or more of their length into a tube 1–2 mm long, bicoloured anthers, and a short style, ± 6 mm long.

The distinctive combination of narrow leaves and a long style separates *C. ramosissima* from the forms of *C. orchidiformis* with unpatterned tepals. The two species share smaller upper lateral anthers and otherwise resemble one another very closely although they are readily distinguished in fruit, as *C. ramosissima* has much smaller, subglobose or ovoid capsule, 7–10 mm long vs. the large, oblong or ellipsoidal capsules, 12–15 mm long of *C. orchidiformis*. Although *C. orchidiformis* mostly has the style shorter than the lower anthers, occasional collections (see below) have elongated styles like those of *C. ramosissima*. In the absence of fruits, such aberrant plants can be identified by their broader, soft-textured leaves and slightly larger anthers, tinged greyish distally. The two species are essentially allopatric, overlapping in their distribution only in the Richtersveld, where *C. ramosissima* is restricted to the mountainous central region whilst *C. orchidiformis* extends around the fringes.

*Representative specimens*


2. **Cyanella marlothii** J.C.Manning & Goldblatt, sp. nov.

*Type.*—Northern Cape, 2817 (Vioolsherd): sandy flats between Jasper’s werf and Doornpoort [Doringpoort Farm at W foot of Ploeberg], (–CA), 26 Aug. 1925, R. Marloth 1211 (PRE, holo.).

Plants 200–350 mm high. *Corms* moderately deep-seated, 15–30 mm diam., tunics of coarsely netted, wiry...
fibres, extending shortly into a fibrous neck to 20 mm long, pale brown or grey. Basal leaves 4–6, suberect, linear or linear-lanceolate, 50–100 × 2–6 mm, acute to attenuate, canalicate or involute, with prominent mid-rib and ribbed veins abaxially, firm-textured, glabrous, margins ± undulate, sparsely scabridulous-ciliolate. Inflorescence a moderately dense raceme up to 20-flowered, with up to 2 branches, lower flowers 0.5–0.6 × pedicel length apart; pedicels suberect, deflexed at bracteole, mostly 20–30 mm long; bracteoles inserted in upper third. Flowers facing outwards, pale mauve (‘blue’) with darker veins, presumably fragrant; tepals spreading, outer elliptic, 10–12 × 2–3 mm, apiculate, inner oblanceolate, 10–12 × 2–3 mm, narrowed below. Stamens dimorphic, 3 + 3; filaments erect but deflexed apically, 2–3 mm long, connate halfway or more into cylindrical tube 1–2 mm long; posterior anthers ± sagittate, outer smaller, 1.5–2.0 mm long, median 2.0–2.5 mm long, yellow but greyish or mauve distally, anterior anthers 3–4 mm long, yellow basally but greyish or mauve in distal 2/3. Ovary half-inferior; style medi-ally deflexed, ± 6 mm long, extending shortly beyond anthers. Capsules subglobose, 6–7 mm diam., 3-lobed. Seeds unknown. Flowering time: Aug.–Sept. Figure 6E.

Distribution and ecology: thus far known from a single collection from sandy flats near the Ploegberg, south of Kuboes in the Richtersveld (Figure 7).

Diagnosis and relationships: this distinctive species has the 3 + 3 arrangement of stamens that characterizes sect. Trigella, but is distinguished from other members in the section by having the filaments of all six stamens connate for half to two-thirds of their length into a cylindrical or conical tube that completely encloses...
the ovary. Although the species is based on just a single collection, this comprises three essentially identical individuals. These plants were included in *C. orchidiformis* until now, despite their unique androecium. In this context it is significant that Marloth, who also collected true *C. orchidiformis* from Steinkopf on the same trip as *C. marlothii*, correctly identified the former but treated the latter as *C. capensis* (now *C. hyacintoides*), a clear indication that he considered the Ploegberg collection to be distinct from *C. orchidiformis*, although he was misled by the connate filaments into misidentifying it as *C. hyacintoides*. The latter does not occur in the Richtersveld, and is in any event immediately distinguished by its 5 + 1 arrangement of anthers and by the spreading-geniculate pedicels.

Among the members of sect. *Trigella*, *C. marlothii* resembles *C. ramosissima* in its narrow leaves, 2–6 mm wide, pale mauve or blue flowers with darker veins, and apparently ± globose capsules, but is separated from it by its smaller flowers with tepals 10–12 vs. 13–20 mm long, bicoloured vs. plain yellow anthers, and shorter style, ± 6 mm long and only slightly longer than the anthers vs. 10–15 mm long and ± twice as long as the anthers.

We have considered the possibility that the collection may be hybrid between a member of sect. *Trigella* (*C. cygnea* is recorded from the Kuboes area) and *C. hyacintoides*, but discount this in view of the consistent appearance of the plants and the lack of other intermediate characters. This possibility did not suggest itself to Marloth, who did not record any potential parent species at the site. The absence of additional collections of the taxon is unfortunate but not unique—no further plants of *W. gracilis* have been recorded from the Richtersveld since Marloth's collection on 29 August 1925, just three days after his collection of *C. marlothii* (but see this species for further comment).


Plants 150–500 mm high. Corms moderately or very deep-seated, 15–30 mm diam., tunics of coarsely netted, woody fibres, sometimes connate below into flat claws, extending shortly into a fibrous neck up to 20 mm long, chestnut-brown. Basal leaves 4–6, suberect or spreading, lanceolate, 70–250 × 10–25(–30) mm, acute to attenuate, plane or canaliculate, with prominent midrib abaxially, soft-textured, glabrous, margins plane or undulate, smooth or ciliolate-scabridulous. Inflorescence a moderately dense raceme up to 35-flowered, with 1 or 2 branches, lower flowers 0.5–0.8 × pedicel length apart; pedicels suberect and deflexed at bracteole, mostly 15–30 mm long; bracteoles mostly inserted in upper third or quarter, sometimes in lower half or quarter. Flowers facing outwards, pink or mauve with darker veins, sometimes with darker centre, or with paler centre variously speckled with dark pink, the whole outlined with darker shading, fragrant; tepals spreading, outer elliptic, (8–)10–15(–20) × 4–5 mm, apiculate, inner oblong-elliptic, (8–)10–15(–20) × 5–6 mm, narrowed below. Stamens dimorphic, 3 + 3; filaments of posterior cluster arcuate to geniculate-sigmoid, 2–5 mm long, connate at extreme base only, ± evenly thick throughout, yellow with white base, anthers ± sagittate, outer smaller, 1–2 mm long, median 2–3 mm, yellow, but grey to purple distally; filaments of anterior cluster deflexed, 1.5–2.5 mm long, connate at extreme base, anthers 5–6 mm long; pale yellow at base, greyish or purple distally. Ovary half-oblunt; style media! deflexed, (4–)5–13 mm long, ± as long as or extending well beyond anthers. Capsules erect, ovoid-ellipsoid to oblong, 14–25(–30) × 8–10 mm, pale with purplish reticulation. Seeds ovoid-ellipsoid, 3–4 × 1.5–2.0 mm, glossy black, rugose. Chromosome number: 2n = 24 (Ornduff 1979). Flowering time: (mid–)late Jul.–late Sept. Figure 6A, B.

**Distribution and ecology**: occurring along the western escarpment, from just north of Steinkopf in northern Namaqualand to Citrusdal in the Olifants River Valley (Figure 7). Collections from the Richtersveld cited under this species by Scott (1991) are referable to *C. cygnea*, evident from their filiform, sigmoid upper filaments and smaller anthers. Plants grow mostly in clay or loamy soils, often in rock crevices in granite or sandstone, where they benefit from extra moisture through run-off among rocks along the courses of seasonal streams, especially in Namaqualand.

**Diagnosis and relationships**: the most common and widespread of the three species of sect. *Trigella*, *C. orchidiformis*, is recognized by its lanceolate leaves, 10–25 mm wide, and racemes of pink to mauve flowers, mostly darker or patterned toward the centre, with the anthers partially or almost wholly greyish or purple, and large, ovoid-ellipsoid fruits, 14–25 mm long. The three species are essentially parapatric or allopatric, although both *C. cygnea* and *C. orchidiformis* have been collected near Steinkopf (*Marloth 6761, 6761A*). An exceptionally large-flowered variant with tepals 20 × 6–7 mm has been collected on the Gilberg Pass, growing in sandstone soil after fire (*Goldblatt & Porter 13190*), and may be polyploid.

*Cyanella orchidiformis* is closely allied to *C. cygnea*, with which it shares the distinctive large fruits, patterned perianth, and coloured anthers, but from which it is distinguished by its generally larger flowers, with tepals mostly 10–13 mm long vs. 8–10 mm long, and its unex-

![FIGURE 7.—Distribution of *Cyanella marlothii*, ○; *C. orchidiformis*, ●](image-url)
exceptional stamens. The upper filaments in *C. orchidi-formis* are arcuate or weakly geniculate, without a bul-bose base and not evidently filiform in the distal half, and the lower anthers are relatively large, 5–6 mm long. The style is very variable in length, mostly 5–10 mm long, but occasionally up to 15 mm long. In contrast, *C. cygnea* has mostly smaller flowers, with tepals 8–10 mm long and very distinctive stamens, with the upper filaments geniculately sigmoid and sharply narrowed and filiform in the distal half, with much smaller lower anthers, 2.5–3.0 mm long, and a short style 3–4 mm long. The range of *C. orchidi-formis* is largely to the south and east of *C. cygnea* but both species have been collected near Steinkopf.

The relatively broad leaves, 10–30 mm wide, and large capsules, readily distinguish *C. orchidi-formis* from *C. marlothii* and *C. ramosissima*, which have narrow leaves 2–8 mm wide and smaller, subglobose-ovoid fruits 7–10 mm long.

**Vernacular name:** waterraap.

**Representative specimens:**


**Long-styled morphs**


Plants (150–)200–500 mm high. *Corms* moderately or very deep-seated, 15–30 mm diam., tunics of coarsely netted, woody fibres, sometimes conenate below into flat claws, extending shortly into a fibrous neck up to 20 mm long, chestnut-brown. *Basal leaves* 4–6, suberect, lanceolate, 80–200 × 10–20(–25) mm, acute to attenuate, plane or canalicate, with prominent midrib and ribbed veins abaxially, soft-textured, glabrous, margins smooth or ciliate-scabridulous. *Inflorescence* a dense or moderately dense raceme up to 35-flowered, with 1–4 branches, lower flowers 0.2–0.5 × pedicel length apart; pedicels suberect, deflexed at bracteole, mostly 15–30 mm long; bracteoles mostly inserted in upper third or quarter. *Flowers* facing outwards, pink with paler centre variously speckled with dark pink, the whole outlined with darker shading, fragrant; tepals spreading, outer elliptic, 8–10 × 4–5 mm, apiculate, inner obovate, 8–10 × 5–6 mm, narrowed and short-clawed below. *Stamens* dimorphic, 3 + 3; filaments of posterior cluster geniculate-sigmoid, 2–5 mm long, distally filiform and strongly flexuose, swollen basally, conenate at extreme base only, yellow with white base, anthers ± sagittate, 1.5–2.0 mm long; filaments of anterior cluster deflexed, 1.0–1.5 mm long, conenate at extreme base, anthers 2.5–3.0 mm long, pale yellow but greyish in distal half or third. *Ovary* half inferior; style medially deflexed, 3–4 mm long, not extending beyond anthers. *Capsules* erect, ovoid-ellipsoid, (12–)15–20 × 8–10 mm. *Seeds* ovoid-ellipsoid, 3–4 × 1.5–2.0 mm, glossy black, rugose. *Flowering time*: late Aug.–early Oct.–(early Nov.). Figure 6C, D.

**Distribution and ecology:** restricted to the higher-lying parts of northern Namaqualand, where it has been collected in the Richtersveld along the Ploegberg and Stinkfontein Mtns, from Kuboes to Eksteenfontein, near Steinkopf, and along the edge of the escarpment around Komaggas, some 60 km to the south (Figure 8). Plants grow in rocky situations in open succulent karoo shrubland, typically where there is additional moisture such as along watercourses or in gorges.

**Diagnosis and relationships:** closely allied to *C. orchidi-formis*, with which it shares characteristi-cally mottled flowers and large, ovoid-ellipsoid capsules ± 15 mm long, and greyish or purple markings or speckling on the anthers. *Cyanella cygnea* typically has smaller flowers, with tepals 8–10 vs. (8–)10–15(–20) mm long, but is best identified by its stamens. The
strongly geniculate-sigmoid filaments of the posterior (upper) stamens are bulbous at the base and filiform in the distal half, giving them a characteristic flexuous form, the outer pair slightly longer than the median. All three anthers in the posterior cluster are subequal in size, 1.5–2.0 mm long, and the lower anthers are equally larger, 2.5–3.0 mm long. In contrast, the upper stamens in *C. orchidiformis* are ± uniformly thick except at the extreme apex and not evidently flexuous, the outer anthers are slightly smaller than the median, and the lower anthers are larger, 5–6 mm long, sometimes with the median larger than the laterals. The distributions of the two species are largely complementary, with *C. cygneae* occurring to the north and west of *C. orchidiformis*, but they overlap around Steinkopf.

**Vernacular name:** *wildebeet* (wild beet) (Scott 1991).

**Representative specimens**


**II. Section Cyanella**

**Flowers** sometimes enantiostylos; perianth white, yellow, orange, pink to mauve or blue, rarely patterned. **Stamens** 5 × 1; anthers ± oblong. **Ovary**: style sometimes flexed to left or right.

**Series Hyacinthoides** J.C.Manning & Goldblatt, ser. nov.

**Flowers** not enantiostylos; pedicels ± geniculate (horizontally spreading then flexed sharply upwards) or arculate; perianth white, orange, pink, or mauve to blue. **Stamens**: filaments connate halfway or more. **Ovary**: style not flexed sideways. Type species: *Cyanella hyacinthoides* Royen, ex L.

5. **Cyanella hyacinthoides** Royen ex L., Genera plantarum, edn 5: addendum [522] (1754). *C. capensis* L.: 985 (1759), nom. illegit. superfl. *C. pulchella* Salisb.: 249 (1796), nom. illegit. superfl. [Note: Scott’s (1991) lectotypification of *C. pulchella* against Jacquin’s (1776–1777) illustration of *C. capensis* L. is unwarranted and incorrect. There is no indication that Salisbury had any intention other than of replacing Linnaeus’s name with his own.] Type: South Africa, without precise locality, date or collector, ex herb. Royen Herb. Linn. 430.2 (LINN, holo.).

Plants 150–400(–500) mm high. **Corns** deep-seated, 25–30 mm diam., tunics of coarsely netted, wiry or woody fibres, not or extending shortly into a fibrous neck to 20 mm long, pale brown or grey. **Basal leaves** 4–9(–12), suberect or spreading, linear to narrowly lan-

![FIGURE 9.—Distribution of Cyanella hyacinthoides (pubescent forms, ○).](image-url)
been collected on granite, sandstone, and limestone substrates, although it favours loamy or clay soils, where it is most often found as a component of renosterveld or succulent karoo communities. It is tolerant of disturbance and thrives in old lands and along road verges.

**Cyanaella hyacinthoides** is extremely variable in its foliage. Plants typically produce 4–6 lanceolate leaves but some forms may produce up to a dozen linear- involute leaves. These narrow-leaved plants are scattered throughout the range of the species. A more circumscribed ectotype occurs along the higher parts of centralNamaqualand, between Kotzesrus and Springbok. Plants there tend to have the lower leaf surface variously scabridulous or villous, with the hairs restricted to the leaf margins and the adaxial veins and midrib. In extreme forms, the hairs are shaggy and up to 1 mm long but there is a significant variation in the density and length of the vestiture, even within a single locality, from scarcely puberulous to densely villous leaves. A collection from north of Komaggas (Barker 7412) shows a second type of vestiture, with both leaf surfaces closely and evenly puberulous. Populations from elsewhere in the range generally have the leaf surfaces glabrous, but some plants may have the lower surface sparsely and minutely scabridulous along the veins. There is no association between vestiture and other vegetative features, such as leaf width or shape. The development of leaf pubescence in populations from this part of Namaqualand has also been recorded in species of Trachyandra (Asphodelaceae) (Manning & Goldblatt 2007) and Haemanthus (Amaryllidaceae) (Snijman 1984), and appears to represent a widespread ecological strategy.

Tetraploids have been detected among several wild populations of Cyanaella hyacinthoides (Ornduff 1979), and it is thus possible that unusually robust specimens that have been remarked on by various collectors are polyploids.

**Diagnosis and relationships:** Cyanaella hyacinthoides is distinguished by the moderately dense, branched racemes of mauve to blue (rarely white or pink) flowers with 5 + 1 arrangement of stamens with the filaments connate for ± half their length or more. The connate filaments and generally horizontally spreading pedicels serve to distinguish the species from pink-flowered forms of *C. lutea*, in which the stamens are ± free and the pedicels mostly suberect.

The species is closely allied to *C. pentheri*, with which it has been much confused, and the two were treated as conspecific by Scott (1991). They are essentially alike in their inflorescence, although the flowers in *C. pentheri* are typically paler, mostly white to pale mauve, but they differ strikingly in their foliage. The leaves of *C. pentheri* are linear-aristate and canaliculate-involute with margins that are often crispileate and conspicuously ciliate only towards the base with shaggy hairs 2.0–3.0 mm long. Similar long cilia also fringe the upper cataphyll, which is funnel-shaped, and boldly pigmented with deep purple along the edges and veins, giving it a characteristic fenestrate appearance. Although *C. hyacinthoides* is highly variable in its foliage, the species only rarely produces similarly narrow, crisspulate leaves and in such cases they are either glabrous or are ciliate-pubescent along their entire length, with much shorter hairs 0.2–1.0 mm long, and the upper cataphyll is usually unmarked, very rarely (Goldblatt & Porter 11896) purple-fenestrate. Although the two taxa have been recorded growing in close proximity in several localities (see discussion under *C. pentheri*), no intermediates between them have been found.

**Vernacular names:** raap, homotsraap, klipraap.

**Representative specimens**

**Typical form**

Hairy forms


6. Cyanella pentheri Zahlbr. in Annelen des kaiserlichen naturhistorischen Museums 15: 26 (1900). Type: South Africa, [Western Cape], Olifantrivier [Olifants River], Aug. [without year], Penther 400 (W, holo.†).

Neotype: South Africa, [Western Cape], Clanwilliam, Biedouw [Bitouw], Welbedacht Farm, 22 Sept. 1952, A.J. Middelmost 1741 (NBG, neo., designated here; SAM, iso.).

Note: The type of Cyanella pentheri is presumed lost (Scott 1991) but Zahlbruckner’s (1900) description is quite clear and we designated an extant specimen to serve as a neotype.

Plants 100–400 mm high. Corms deep-seated, 25–30 mm diam., tunics of coarsely netted, wiry or woody fibres, extending in a short or very long fibrous or papery neck to 100 mm long, pale brown. Basal leaves (5–)9–17, suberect, often ± twisted or coiled apically, linear, 60–150 × 1–4(–5) mm, attenuate, cancellate-involute, with prominent midrib and ribbed veins abaxially, firm-textured, glabrous or veined puberulous abaxially, margins straight or ± undulate or crispulate, conspicuously ciliate in basal parts only with shaggy hairs 2.0–3.0 mm long but glabrous distally; upper caffalyl prominent, with crispulate margins villous as in leaves, strongly flushed purple towards edge and along veins, thus fenestrate, sometimes also villous on veins. Inflorescence a moderately dense raceme up to 25-flowered, simple or up to 4-branched, lower flowers 0.3–0.6 × pedicel length apart; pedicels geniculate, horizontal in basal half or 2/3 then abruptly flexed upwards at ± right angles, mostly 20–30 mm long; bracteoles mostly inserted between lower and upper third, rarely sub-basal. Flowers facing outwards, white to pale mauve or blue, fragrant; tepals spreading, ovate, 7–11 × 3–4 mm, apiculate. Stamens dimorphic, 5 + 1; filaments of posterior cluster 2.0–3.5 mm long, connate ± 1/3 to 2/3 into tube 1.0–1.5 mm long, yellow, anthers 1.5–2.5 mm long, yellow; anterior stamen with filament ± 1 mm long, connate to upper cluster for ± half length, anther 2.5–3.5 mm long, yellow. Ovary half-inferior; style medially deflexed, 3–4 mm long, not extending beyond anthers. Capsules erect on geniculate pedicels, subglobose, 5–6 mm diam., 3-lobed and retuse. Seeds unknown. Flowering time: late Aug.—early Oct.

Distribution and ecology: Cyanella pentheri has a restricted distribution through the middle reaches of the Olifants River Valley from north of Citrusdal to Klawer, extending along the foot of the Gilberg onto the Bokkeveld Escarpment, and inland to the Bitouw and Doring River Valleys (Figure 10). Plants favour rocky places, often sandstone, mainly in arid fynbos.

Diagnosis and relationships: Cyanella pentheri has mostly been treated as conspecific with C. hyacinthoides, essentially because of the confusion between true C. pentheri and what we regard as pubescent forms of C. hyacinthoides. Florally, the two species are certainly alike in their moderately dense, branched racemes of spreading, white or mauve to blue flowers with 5 + 1 arrangement of stamens with the filaments connate for ± half their length or more, but they differ significantly in their foliage. The leaves of C. pentheri are consistently linear and cancellate-involute, mostly 1–4 mm wide, with margins that are conspicuously ciliate only towards the base with long, shaggy hairs 2.0–3.0 mm long. Similar, long cilia also fringe the upper caffalyl, which is funnel-shaped, and strikingly pigmented with deep purple along the edges and veins, giving it a characteristic fenestrate appearance. The leaves of C. hyacinthoides, in contrast, are mostly lanceolate and 4–15 mm wide, rarely narrower, with margins either smooth or ciliolate-pubescent along their entire length, with much shorter hairs 0.2–1.0 mm long, and the upper caffalyl is usually unmarked. Pubescent forms of C. hyacinthoides from central Namaqualand have leaves that are variously puberulous to villous, but never with the long cilia characteristic of C. pentheri.

The variation in vestiture in C. hyacinthoides is not correlated with leaf shape, unlike the situation in C. pentheri. This is compelling evidence that C. pentheri represents a distinct genotype, which is further corroborated by the fact that the vegetative differences between the two species are maintained wherever the two have been collected together, notably north of Klawer at Zandkraal Farm (Barker 5648 vs Barker 5662), Welbedacht Farm in the Bitouw Valley (Middelmost 1741 vs Johnson 537) and Clanwilliam (Perry 3526 vs Barker 4771). We have examined both taxa growing together just outside Clanwilliam ourselves and at none of these localities have we found intermediates between them.

Vernacular name: klipraap.

Representative specimens

NORTHERN CAPE.—3119 (Calvinia): Nieuwoudtville, Willens River Farm, (–AC), Sept. [without year], Leipoldt 789 (NBG); Nieuwoudtville, hills near Groenrivier, (–AC), Sept. [without year], Leipoldt 790 (NBG).
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Plants up to 500 mm high. Corms shallow or moderately deep-seated, 20 mm diam., tunics of papery or leathery layers, not extending into neck, pale whitish brown. Basal leaves ± 5 or 6, suberect, linear-lanceolate or narrowly lanceolate, 200–350 × 10–15 mm, attenuate below into claws, extending shortly in a neck to 30 mm long, rarely into a fibrous neck up to 100 mm long, brown. Capsules or above, only rarely near the base. The two taxa are ecologically separated, with C. hyacinthoides favouring better drained, sandy or gritty soils. In perianth colour, C. aquatica might be confused with yellow-flowered C. lutea, but that species has suberect pedicels with the bracteoles inserted ± midway along, filaments that are ± free to the base, and a laterally deflexed style. Cyanella lutea is also ecologically separated, favouring fine-grained clay soils in renosterveld or drier karroid vegetation.

Representative specimens


Series Luteae J.C.Manning & Goldblatt, sess. nov.

Flowers ± enantiomorphic; pedicels suberect; perianth white, yellow, or pink. Stamens: filaments free, anthers sometimes spotted or maculate. Ovary: style and lower anther weakly or strongly flexed sideways in opposite directions. Type species: Cyanella lutea L.f.

8. Cyanella lutea L.f., Supplementum plantarum: 201 (1782). Type: South Africa, without precise locality or date, Sparrman s.n. Herb. Linn. 430 L (LINN, holo.!).

Plants (120–)150–350 mm high. Corms moderately to deep-seated, 20–25 mm diam., tunics of coarsely netted, fibrous, leathery or woody fibres, sometimes conuate below into claws, extending shortly in a neck to 30 mm long, rarely into a fibrous neck up to 100 mm long, brown. Basal leaves 4–15 mm, suberect or spreading, linear-hemiterete to lanceolate, 30–200–(250) × 2–15–(20) mm, acute to attenuate, leathery, plane or canaliculate, glabrous, margin smooth or ciliolate-scabridulous. Inflorescence a moderate or dense raceme up to 15-flowered, with 1–3 branches congested near base, thus emerging from among leaves, rarely with accessory branchlets and thus paniculate, lower pedicels 0.2–0.8 × their length apart; pedicels suberect, rarely arcuate or almost geniculate, 15–30–(50) mm long; bracteoles mostly inserted between ± halfway and upper third, sometimes in basal third or sub-basal. Flowers ±...
enantiomorphic, facing outwards, yellow or pink to purple, usually flushed darker on reverse, with dark veins, fragrant; tepals spreading, outer oblong-elliptic, 10–15–18 × 2–4 mm, apiculate, inner elliptic-ovate, 10–15–18 × 3–7 mm, acute, narrowed basally or very short-clawed. Stamens dimorphic, 5 + 1; filaments of posterior cluster 2.5–4.0 mm long, connate only at extreme base, ± linear, yellow, anthers 2–4 mm long, yellow, usually finely spotted black or maroon; anterior stamen with filament deflexed ± laterally, 4–5 mm long, linear, connate to upper cluster at extreme base only, anther 4–7 mm long, thus ± twice as large as upper, yellow, brown, or mauve. Ovary half inferior; style ± laterally deflexed to left or right opposite lower stamen, 6–10 mm long, not extending beyond lower anther. Capsules erect, subglobose-retuse, 6–8 mm diam., 3-lobed. Seeds ovoid, ± 2 mm diam., rugulose. Chromosome number: 2n = 24 (subsp. lutea: Ornduff 1979). Flowering time: mainly Aug.–Nov. Figures 6K, L; 12.

Distribution and ecology: the most widely distributed species in the genus, C. lutea, extends through the winter rainfall region of southern Namibia and South Africa and around the interior margin of the central plateau but is absent from the central and Great Karoo (Figure 13).

Pink-flowered plants, often with narrower leaves, have been distinguished taxonomically several times, but differ consistently from the typical yellow-flowered form only in perianth colour. Baker (1871) initially recognized var. rosea from the Eastern Cape but subsequently (Baker 1880) changed his mind. This decision was followed by Scott (1991). However, the two colour morphs are geographically segregated: pink-flowered plants are recorded from the edges of the winter rainfall region into interior southern Africa, typically in sandy soils; and yellow-flowered plants are restricted to the southwestern Cape and nearby, on clay soils. We accordingly treat them here as distinct subspecies.

Diagnosis and relationships: distinguished from other members of sect. Cyanella by its racemes of pink or yellow, ± enantiostylos flowers with almost free filaments, connate only at the extreme base, and the lower anther ± twice as large as the upper anthers. Yellow-flowered plants are readily recognized by their colour but pink-flowered plants could be confused with C. hyacinthoides around Springbok in Namaqualand, where both occur. Cyanella hyacinthoides is recognized by its partially connate upper filament cluster, with the lower anther mostly less than twice as long as the upper, and by its spreading-geniculate pedicels. Subspecies rosea has also been confused with C. ramosissima (sect. Trigella), but the arrangement of the stamens is quite different in the two species.

Key to subspecies

1a Leaves mostly lanceolate, (2–)5–15–20 mm wide; perianth pale to golden yellow, rarely orange, often flushed reddish on reverse; plants from southwestern Cape, from Nieuwoudtville to Uitenhage . . . . . . . . . . . . . . . . . . . 8a. subsp. lutea

1b Leaves linear to linear-lanceolate, 2–10–12 mm wide; peri-

FIGURE 12.—Cyanella lutea: A, flowering plant; B, half-flower; C, capsule; D, seed. Scale bar: A–C, 10 mm; D, 2 mm. Artist: John Manning.

FIGURE 13.—Distribution of Cyanella lutea subsp. lutea, ●; C. lutea subsp. rosea, ○.
anth pink to purple; plants from southern Namibia and northern Namaqualand across interior of South Africa into Eastern Cape as far as Humansdorp. 8b. subsp. rosea

8a. subsp. lutea

C. racemosa Schinz: 394 (1895). Type: South Africa, [Western Cape], in arenosis [sandy] Camp Ground prep. [proper], Cape Town, 12 June 1892, Schlechter 839 (Z, holo.; PRE, iso.).

C. lutea forma angustior Zahr.: 27 (1900). Type: South Africa, [Western Cape], Caledon, Oct. [without year], Penther 494 (W, holo.†).

Leaves 4–10, mostly lanceolate, rarely linear, (2–)5–15(–20) mm wide. Flowers pale to golden yellow, often flushed reddish on reverse or tinged orange.

Distribution: endemic to winter rainfall South Africa, where it has been recorded from the Bokkeveld Escarpment and southern Roggeveld to the Cape Flats and flushed reddish on reverse or tinged orange.

Representative specimens


Note: Scott (1991) was of the opinion that no material of Cooper’s collection had been preserved and thus lectotypified the name against the illustration in Refugium Botanicum, which was drawn from plants collected and cultivated by Thomas Cooper. There exists, however, a specimen at Kew, collected by Cooper in 1860 at Queenstown in the Eastern Cape where this form has since been re-collected, and labelled with the name Cyanella rosea. There seems no reason to doubt that it represents the original collection from which the cultivated plants were derived. This material, as the holotype, takes precedence over the illustration (McNeill et al. 2006: Art. 9.10 & 9.17). Baker’s (1871) citation of the Ecklon manuscript name, Cyanella rosea Eckl., which appeared as a printed label on some herbarium collections, including Eckl 255 (NBG), is a clear indication that the correct author citation for the epithet is Eckl. ex Baker.

C. lineata Burch.: 589 (1812). Type: South Africa, Beechuanaland [Northern Cape], near Moshowa [Moshaweng] River, without exact date [1811–1812], Burchell 2256-2 (K, holo.).

C. odoratissima Ker Gawl.: t. 1111 (1827). Type: South Africa, Cape of Good Hope, without precise locality, date or collector, cultivated in Tate’s nursery, London, apparently not preserved, illustration in Ker Gawl., The Botanical Register 13: t. 1111 (1827). [Note: Scott’s (1991) attribution of the name to Lindley is incorrect, as John Bellenden Ker [-Gawler] wrote the text for the first 14 volumes (Staffel & Cowan 1976), and John Lindley only assumed authorship from vol. 15.]


Leaves 6–12, linear-hemiterete to linear-lanceolate,
2–10(–12) mm wide. Flowers pale to deep pink or purple. **Flowering time:** mainly Aug.–Sept. in Namaqualand and Bushmanland; Oct.–Dec. in the interior and Eastern Cape.

**Distribution:** recorded from central Namaqualand around Springbok and the Huib-Hoch Plateau in southern Namibia, inland through Bushmanland along the Orange and Vaal Rivers as far as Kuruman in Northern Cape and Smithfield in the southern Free State, thence southwards through the eastern Upper Karoo to Humansdorp (Figure 13). Plants have been recorded mainly from sandy, sometimes calcareous, flats in Nama-Karoo shrubland or drier grassland, in the Kuruman area typically beneath small bushes. The subspecies is relatively poorly documented for such a large range.

**Diagnosis:** distinguished by its generally narrower, often grass-like leaves 2–12 mm wide, and its pink perianth. Plants from NamaquaLand-Bushmanland and southern Namibia are especially distinctive in their very small stature, numerous, semi-terete leaves, and ± congested inflorescence branching near the base, giving them a characteristic caespitose appearance.

**Representative specimens**

FREE STATE.—3026 (Alwil North): Smithfield, (–BA), Oct. [without year or collector], STE12787 (NBG).


Plants 80–200 mm high. **Corns** deep-seated, 15–25 mm diam., tunic of coarsely netted fibres, extending into neck up to 50 mm long, pale brown. **Basal leaves** ± 10–20, erect, filiform to linear, (40–)50–100 × 0.5–3.0 mm, attenuate, leathery, bright green, glabrous. **Inflorescence** a highly congested, simple raceme such that flowers apparently solitary among leaves; pedicels suberect, (80–)100–200 mm long; bracteoles either subbasal or inserted in upper half. **Flowers** enantiomorphic, facing outwards, white or pale pink or pale yellow, fragrant; tepals spreading, cucullate, outer elliptic, 12–20 × 5–7 mm, recurved-apiculate, inner ovate, 12–20 × 7–12(–15) mm, acute, narrowed basally or short-clawed, claw up to 1 mm long. **Stamens** weakly dimorphic or submonomorphous, 5 + 1; filaments of posterior cluster 3–5 mm long, connate only at extreme base, awl-shaped, white, anthers 3.5–5.5 mm long, yellow, sometimes marked with black spot on upper surface near base, sometimes cohering; anterior stamen with filament deflexed laterally, 3–4 mm long, awl-shaped, connate to upper cluster at extreme base, anther 4–6 mm long, yellow. **Ovary** half-inferior; style laterally deflexed opposite lower stamen, 7–9 mm long, not extending beyond lower anther. **Capsules** erect, ellipsoid, 13–15 × 7–8 mm, 3-lobed. **Seeds** ovoid, ± 2 mm diam., rugulose. **Chromosome number:** 2n = 24 (subsp. flavescens: Orn.duff 1979). **Flowering time:** (late Aug.–mid-Sept.–mid-Oct.)(Nov.). Figures 6M, N; 14.

**Distribution and ecology:** the species has a scattered distribution along the western mountains in Western Cape, where it is known from the Bokkeveld Escarpment, the Cedarberg and Olifants River Mtns, and the base of the Swartruggess (Figure 15). These three areas of occurrence correspond to the distribution of the three subspecies that we recognize. **Cyanella alba** is restricted to clay soils in renosterveld shrubland.

**Diagnosis and relationships:** one of the easiest species to identify on account of its highly congested inflorescence axis with extremely elongate pedicels, the flowers thus apparently borne on 1-flowered peduncles rather than in a raceme. The raceme is never branched, and up to a maximum of nine flowers are produced, thus very much fewer than in other species. The flowers are strongly enantiostylos; either white or pale pink with uniformly yellow anthers, or pale yellow with maculate anthers. These colour morphs, which are geographically segregated, correlate with the position of the bracteole on the pedicels, and we recognize them as three subspecies. The large, ellipsoid capsule, 13–15 mm long, is unique in sect. **Cyanella**, resembling those of *C. cygnea* and *C. orchidiformis* in sect. **Trigella**.

**Key to subspecies**

1a Leaves filiform, 0.5–1.5 mm wide; flowers white; bracteoles subbasal, not readily visible among leaves and thus apparently absent .......................... 9c. subsp. minor

1b Leaves linear-filiform, 1–3 mm wide; flowers white or yellow; bracteoles inserted in distal half of pedicel, thus
clearly present:

2a Flowers 3–9 per plant, white or pale pink; anthers uniformly yellow . . . . . . . . . . . . . . . . . . . . . . . . . .  9a. subsp. *alba*

2b Flowers 1–4 per plant, pale yellow or outer tepals white; upper anthers marked with black blotch adaxially near base . . . . . . . . . . . . . . . . . . . . . . . . . .  9b. subsp. *flavescens*

9a. subsp. *alba*

Plants (80–)100–200 mm high. Leaves linear, 1–3 mm wide. Inflorescence 3–9-flowered; pedicels with bracteole in distal half. Flowers white to pale pink. Stamens: anthers uniformly yellow. Figure 14A.

Distribution: endemic to the Bokkeveld Escarpment, from just north of Nieuwoudtville southward to Menzieskraal near Botterkloof (Figure 15).

Diagnosis: characterized by the long pedicels, (80–)100–200 mm long, with the bracteole inserted between one third and three-quarters along, and white or pale pink flowers flushed darker pink on the reverse. The anthers are uniformly yellow, with the upper cluster free or coherent. Plants are often well grown, producing 3–9 flowers. The position of the bracteoles in the distal half of the pedicels distinguishes subsp. *alba* from subsp. *minor* from the Tanqua Basin to the south, which has similar flowers but subbasal bracteoles.

Representative specimens

NORTHERN CAPE.—3119 (Calvinia): N of Nieuwoudtville, Grasberg Farm, (–AC), 16 Sept. 1961, Barker 9457 (NBG); Nieuwoudtville Reserve, (–AC), 8 Sept. 1983, Perry & Snijman 2351 (NBG); ± 15 km S of Nieuwoudtville, Matjiesfontein Farm, (–AC), 13 Sept. 1976, Thompson 2902 (NBG); Lokenberg Farm, (–CA), 26 Sept. 1933, Acocks 17263 (PRE); 4 Sept. 1985, Snijman 905 (NBG); Menzieskraal Farm, (–CA), 29 Sept. 1933, Markotter s.n. (NBG).


Plants 120–200 mm high. Leaves linear-filiform, 1–2 mm wide. Inflorescence 1–4-flowered; pedicels with bracteole in distal 1/2. Flowers pale yellow or outer tepals white. Stamens: anthers yellow, upper five coherent and maculate with dark blotch on upper side near base.

Distribution: restricted to the northern Cedarberg and Olifants River Valley, between Clanwilliam and Wuppertal, and especially common in the Biedouw River Valley (Figure 15).

Diagnosis: a very distinctive taxon recognized by its pale yellow flowers (sometimes the outer tepals white) with the upper anthers coherent and marked on the upper side with a black blotch near the base. Up to four flowers are produced per plant.

Representative specimens


FIGURE 14.—*Cyanella alba*: A, subsp. *alba*, showing distal bracteole; B, subsp. *minor*, showing subbasal bracteole. Scale bar: 10 mm. Artist: John Manning.

FIGURE 15.—Distribution of *Cyanella alba* subsp. *alba*, ●; subsp. *flavescens*, ○; subsp. *minor*, ▲.
Plants 80–150 mm high. Leaves filiform, 0.5–1.5 mm wide. Inflorescence 1–3-flowered; pedicels with bracteoles subbasal. Flowers white to pale pink with darker pink on reverse. Stamens: anthers pale yellow, by the shorter pedicels, mostly 1–3-flowered; pedicels white to pale pink with darker pink on reverse. Stamens: anthers uniformly yellow. Flower 14B.

Distribution: highly localized and known only from just north of Karoopoort in the southern Tanqua Karoo basin (Figure 15).

Diagnosis: distinguished from the typical subspecies, which has similar white or pale pink flowers and uniformly yellow anthers, by the shorter pedicels, mostly < 100 mm (rarely up to 150 mm long) with the bracteoles subbasal and thus difficult to distinguish from the leaves. This led Manning et al. (2005) to conclude that bracteoles were absent, and we were only able to establish the true situation after having the opportunity of dissecting live plants. The plants are typically small in stature, with only 1–3 flowers per plant.

Representative specimens

EXCLUDED SPECIES
Walleria paniculata Fritsch: 493 (1896). Type: Madagascar, Ins. St Marie, without date, Padlay s.n. (GZU, holo.) = Dianella ensifolia (L.) DC. (Hemerocallidaceae) (Perrier de la Bathie 1938).

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REFERENCES