Two new species of *Gladiolus* (Iridaceae: Ixioideae) from South Africa and notes on long-proboscid fly pollination in the genus

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ABSTRACT

Gladiolus rhodanthus is a new species known from a single population on the summit of the Stettynsberg near Villiersdorp in Western Cape, South Africa. The species most closely resembles G. hirsutus and G. caryophyllaceus but differs from both in flower shape and markings and in its ecology and reproductive biology. It forms part of a guild of long-tubed, pink-flowered species including Erica praecox, Pelargonium radiatum and Watsonia paucifolia which are pollinated by an undescribed long-proboscid fly, Moegistorhynchus sp. nov. (Diptera: Nemestrinidae). Gladiolus sekukuniensis is a new species known from three populations south of the Strydpoortberge in Northern Province. It closely resembles G. permeabilis subsp. edulis in vegetative features and in flower form, but differs from it in flower colour and in the elongate perianth tube. These floral features are apparently adaptations to pollination by long-proboscid flies.

INTRODUCTION

Arguably the largest genus in the family Iridaceae, Gladiolus contains some 260 species distributed throughout Africa and Eurasia as far east as Afghanistan, but its greatest centre of diversity is in southern Africa. Some 165 species occur in the subcontinent, of which 159 are endemic there (Goldblatt & Manning 1998). Within the subcontinent several centres of endemism have been identified (Goldblatt & Manning 1998). By far the greatest number of species occurs in the southwestern corner, the centre of the southern African winter rainfall region. This is an area of high topographic and edaphic diversity in which local endemism is highly developed. Many of these endemics are restricted to a single isolated massif or mountain range. It is not altogether surprising, therefore, that a new species of Gladiolus should be discovered on a high mountain barely four months after the publication of a comprehensive revision of the genus (Goldblatt & Manning 1998). A second centre of diversity, the Wolkberg centre, lies at the opposite end of the subcontinent in the highlands of Mpumalanga and Northern Province. This is a region of great geological complexity, and local endemism within the genus here is largely the consequence of the high edaphic diversity. Substrates favouring endemism include sandstones or quartzites, dolomite and serpentine. The discovery of another apparent edaphic endemic from the northern part of the region emphasises the importance of substrate in promoting speciation in Gladiolus throughout the subcontinent.

Species of *Gladiolus* are highly diverse in floral form and much of this variation is related to their pollination biology. Although bees are known or inferred to pollinate Gladiolus rhodanthus *J.C.Manning & Goldblatt*, sp. nov. Plantae 300–500 mm altae, cormo globoso 18–25 mm diametro tunicis fibris tenuibus verticalibus, foliis 3 pubescentibus, folio infimo basali lamina lineari 1.5–2.0 mm lata, costa incrassata marginibus vix incrassatis, caule eramoso, spica leviter flexuosa 2–5-flora, bracteis 26–45 mm longis, floribus atroroseis tepalis inferioribus stria albida hastiformi ornatis, tubo perianthii oblique infundibuliformi 25–36 mm longo, tepalis inaequalibus lanceolatis, tepalo dorsali 35–40 × 19–24 mm, inferioribus 27–30 × 11 mm, filamentis 15–17 mm longis, antheris 8–9 mm longis.

TYPE.—Western Cape, Villiersdorp Dist., summit of Stettynsberg, 12 Jan. 1999, *Manning & Paterson-Jones* 2207 (NBG, holo.; K, MO, PRE).

Plants 300–500 mm high. Corm globose, 18–25 mm diam., tunics of medium-textured to fine vertical fibres, accumulating with age and forming a neck around base of stem. Stem erect, flexed outward above sheath of second leaf and inclined ± 30°, unbranched, 1–2 mm diam. below spike. Cataphylls pale and membranous, the uppermost dark green or purple above ground or sometimes dry. Leaves 3, lower one or two basal, the second of these

about 56% of the species in the genus (Goldblatt et al. 1998), one of the most important pollinators of the remainder are long-proboscid flies in the families Nemestrinidae and Tabanidae. This pollination strategy is uniquely well developed in southern Africa and numerous late spring- and summer-flowering plant species throughout the subcontinent have exploited it (Goldblatt & Manning in press). Southern African species of Gladiolus pollinated by long-proboscid flies typically have unscented, long-tubed cream or pink flowers marked on the lower tepals with red (Goldblatt & Manning 1998, 1999). The flowers of both species of Gladiolus described here conform exactly to this pattern and although pollination by long-proboscid flies has been confirmed in only one of the two species, it is inferred to occur in the second.

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sheathing lower half of stem, pubescent throughout, lowermost longest with blade reaching to between base and apex of spike, sometimes becoming dry at flowering time, the second with blade rather short and reaching upper third of stem, blades plane, more or less linear, 3-6 mm wide, midrib thickened and raised and a second pair of veins lightly thickened, margins scarcely thickened, the uppermost leaf inserted on upper third of stem, short, sheathing for half to two thirds of its length, blade vestigial, pubescent. Spike inclined, lightly flexuose, 2- to 5-flowered; bracts green or flushed brownish above, outer 26-45 mm long, acute, inner two thirds or rarely about as long as outer, lightly notched. Flowers deep pink, lower three tepals each with a spear-shaped whitish median streak in lower half edged in dark pink, especially in upper half, sometimes darker edging expanded transversely across entire width of upper laterals, throat white with a few dark pink streaks, unscented; perianth tube 25-36 mm long, cylindrical below for 20-28 mm, obliquely expanded in upper 5–7 mm, shortly exceeding bracts; tepals lanceolate, unequal, dorsal largest, inclined over stamens, 35–40 × 19–24 mm, upper laterals slightly shorter, $30–38 \times 13–19$ mm, recurved in upper half, lower three tepals joined to upper laterals for 5 mm and to one another for 1-2 mm, \pm horizontal below, sharply flexed downward in middle, $27-30 \times 12-13$ mm, in profile lower tepals exceeding upper by 5-10 mm. Filaments 15-17 mm long, exserted 8-10 mm from tube; anthers 8-9 mm long, light mauve; pollen cream-coloured. Ovary oblong, ± 6 mm long; style arching over stamens, dividing at or slightly beyond apices of anthers, branches spreading, 5-7 mm long. Capsules ellipsoid, $20-22 \times 8-9$ mm. Seeds broadly and evenly winged, golden-brown, 5.5-7.0 × 4 mm. Chromosome number: unknown. Flowering time: late December to mid-January. Figure 1; Plate 1.

Distribution and biology: Gladiolus rhodanthus is known from a single large population on the Stettynsberg near Villiersdorp (Figure 2). The plants are restricted to broken sandstone cliffs on warm north-facing slopes at an altitude of 1 800 m where the corms are wedged in cracks in a peaty loam. Frequent summer cloud driven by strong southeasterly winds is a feature of many of the high mountains in the southwestern Cape. At this altitude and in this situation the soil around the corms of G. rhodanthus is still moist in the middle of summer when the plants flower.

The flowers of *Gladiolus rhodanthus* are pollinated by the fly, *Moegistorhynchus* sp. nov. (Nemestrinidae) which has a slender proboscis \pm 20 mm long. There is a close fit between the shape of the flower and the body of the fly. The head and thorax of the fly fit snugly into the upper part of the tube when its proboscis is fully inserted into the lower part. In this position the dorsal thorax brushes against the anthers and style branches while it forages for nectar held in the lower third of the tube.

Several other plant species with long-tubed, similarly coloured flowers co-occur with *G. rhodanthus* and are also pollinated by this fly. They include *Erica praecox*, *Pelargonium radiatum* and *Watsonia paucifolia*. The convergence in flower colouring and perianth length between these plant species at this locality is a striking example of the effect that specialist pollinators can have

on flower form. At the time of its description, the longtubed flowers of W. paucifolia were contrasted with the funnel-shaped blooms of the closely related species W. distans which was thought to be pollinated by bees (Goldblatt 1989). It was already then recognised that the tubular flowers of W. paucifolia were probably specialised for pollination by a different agent, but no information on its pollination biology was available. The recent collection of the pollinator and associated guild members has vindicated this idea. More than one plant species which share a single long-proboscid fly as the pollinator often co-occur and converge in their floral morphology to form a local guild of species (Manning & Goldblatt 1996, 1997). Because of the potential dangers of interspecific pollen transfer in such guilds, pollen is invariably placed by different guild members on different parts of the pollinator's body. This is clearly demonstrated in the Stettynsberg guild: G. rhodanthus deposits pollen on the dorsal surface of the thorax, W. paucifolia on the top of the head, E. praecox on the face and P. radiatum on the underside of the thorax.

History: the species was apparently first encountered by botanists Ted and Inge Oliver in December 1997 on an expedition to collect a species of Erica high on the Stettynsberg to the north of Villiersdorp. Unfortunately no specimens were collected but the following year they revisited the locality accompanied by the natural history photographer, Colin Paterson-Jones, who collected a single plant. This specimen was quite unlike any known species of Gladiolus and another expedition was immediately organised in order to examine the plants in the field and to collect the type material. The Stettynsberg is one of the highest mountains in the greater Hottentots Holland chain, reaching just over 1 800 m at the summit, and until recently has not been accessible except by foot. The late flowering of G. rhodanthus is probably the reason that it was not seen by the indefatigable Cape botanist Elsie Esterhuysen, who first visited the mountain in 1948, and only a chance encounter with spent plants of Erica schoemannii in September 1998, prompted the Olivers to revisit the mountain in December.

Diagnosis and relationships: the three superposed leaves with hairy sheaths and hairy blades with a welldeveloped pair of secondary veins place G. rhodanthus in series Linearifolius of section Linearifolius. This series now contains 12 species, all restricted to sandstone-derived or granitic soils in the winter rainfall region. Radiation in the series is associated with extensive floral adaptation for specialised pollination strategies. In addition several species flower unusually late in the season during the summer, the dry season in most of Western Cape. Within the series the relationships of G. rhodanthus are less clear. Although most likely to be confused with the short-tubed and smaller-flowered G. hirsutus Jacq., the similarities between the two species are largely plesiomorphic and G. rhodanthus may be more closely allied to the species with an elongate perianth tube such as G. caryophyllaceus (Burm.f.) Poir. or G. guthriei F.Bolus.

Gladiolus rhodanthus is readily distinguished from the two other South African species of Gladiolus with well-developed hairy leaves and pink flowers, G. hirsu-

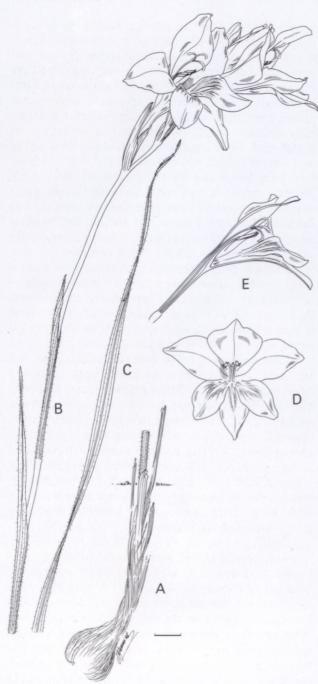


FIGURE 1.—Gladiolus rhodanthus. A, corm with cataphylls; B, flowering spike; C, leaf; D, flower, front view; E, half-flower. Scale bar: 10 mm. Artist: John Manning.

tus or G. caryophyllaceus, by the shape and markings of its flowers and by its late flowering time. Intermediate between these two species in size, the flowers of G. rhodanthus differ from both in their elongate perianth tube, 25-36 mm long, which is cylindrical for most of its length and flares only in the upper 5-7 mm, the lanceolate and acute tepals with plane margins and the median white lozenge-shaped marking outlined with red on each of the lower tepals. The flowers of G. hirsutus and G. caryophyllaceus are obliquely funnel-shaped and flared in the upper half, the tepals are ovate and obtuse, usually with undulate margins, and the lower tepals are irregularly streaked and spotted with red on a pale background. Although nearest G. caryophyllaceus in flower size, G. rhodanthus is also readily separated from this species by its unthickened leaf margins and shorter filaments, 15-17 mm long versus 22-27 mm long. It is most

likely to be confused with *G. hirsutus* but this species has shorter bracts, 18–26 mm long versus 26–45 mm long, and shorter filaments, 11–13 mm long versus 15–17 mm long. In addition *G. rhodanthus* is distinct from these species in its habitat on broken cliffs at high altitude and late flowering time in December and January. *G. hirsutus* is a common species on stony granite or sandstone slopes and flowers mostly between July and September or rarely in March or April while *G. caryophyllaceus* favours dry habitats on open sandstone or granite slopes or in deep sands and flowers between August and September.

The marked floral differences between these species are linked to differences in their floral ecology. The funnel-shaped flowers of G. hirsutus and G. caryophyllaceus are typical of bee-pollinated species of Gladiolus and those of the former, at least, are visited by species of Apis and Anthophora (Hymenoptera: Apidae) (Goldblatt & Manning 1998; Goldblatt et al. 1998) whereas the more tubular flowers of G. rhodanthus are typical of species which are adapted to pollination by long-proboscid flies. In floral morphology G. rhodanthus is actually similar to another quite unrelated fly-pollinated species, G. virgatus Goldblatt & Manning (section Homoglossum). Shifts between pollinators among related species of Gladiolus are common and occur repeatedly throughout the genus. In this regard it is striking to note the floral similarity between both the bee-pollinated and long-proboscid fly-pollinated members of the species pairs G. hirsutus-G. rhodanthus (section Lineariolius) and G. blommesteinii L.Bolus-G. virgatus (section Homoglossum).

In a genus characterised by pollinator-driven floral diversity, series *Linearifolius* is particularly noteworthy for the frequency of derived pollination strategies (Goldblatt & Manning 1998). Out of the 12 species now recognised in the series only two or three are bee-pollinated, the plesiomorphic pollination strategy for the section and the genus. The remaining species have various derived pollination strategies including pollination by moths, long-proboscid flies, birds and the butterfly *Aeropetes tulbaghia* (L.). This strong shift to derived pollination strategies and, in many cases, late or aseasonal

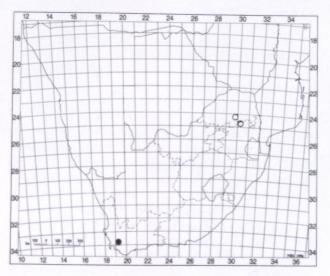


FIGURE 2.—Distribution of Gladiolus rhodanthus, •, and G. sekukuniensis, O, in South Africa.

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flowering times, suggests that section *Linearifolius* entered the winter rainfall region relatively late in the history of the genus, at a time when most of the springflowering, bee-pollinated niches were already occupied by other species of *Gladiolus*, in particular those of sections *Hebea* and *Homoglossum* (Goldblatt & Manning 1998). Both of these sections have diversified strongly in the winter rainfall region, the former mainly on clay soils and the latter on sandstone-derived soils, and contain a preponderance of bee-pollinated species. The discovery of *G. rhodanthus*, another species in series *Linearifolius* which is both late-flowering and adapted to a specialised pollination strategy, provides further support for this hypothesis.

G. rhodanthus can be accommodated in the keys in the recent monograph, Gladiolus in southern Africa (Goldblatt & Manning 1998) by inserting the following couplet into both the key to section Linearifolius and the key to Gladiolus in the winter rainfall region of southern Africa, at leads 14' (p. 53) and 33' (p. 64) respectively.

14'/33' Flowers shades of cream to pink or purple, the lower tepals streaked with dark red to purple; flowering mostly July to January, occasionally April to June

14a'/33a' Perianth tube obliquely funnel-shaped, expanded in upper half; tepals ovate and obtuse, margins usually undulate or crisped, lower tepals irregularly marked with streaks and spots

Material examined

WESTERN CAPE.—3319 (Worcester): Villiersdorp Dist., summit of Stettynsberg, 12 Jan. 1999, (-CD), *Manning & Paterson-Jones 2207* (NBG, holo.; K, MO, PRE).

Gladiolus sekukuniensis *P.J.D.Winter*, sp. nov. Haec species *G. permeabili* subsp. *eduli* (Burch. ex Ker Gawl.) Oberm. similis quoad characteres vegetativos floralesque, sed 600–1 100 mm alta, floribus albis vel pallide carneis atrorubris in medio striatis inodoris, tubo perianthii 25–35 mm longo tepalum dorsalem excedente.

TYPE.—Northern Province, Sekukuniland, Leolo Mountain foothills, Farm Dsjate 249 KT, 800 m E of Motse River, 3 Apr. 1999, *P.J.D. Winter 3283* (NBG, holo.; K, MO, NBG, PRE, UNIN).

Plants 0.6–1.1 m high. *Corm* globose to conic, 8–15 mm diam., mostly producing cormlets on suckers to 100 mm long from base, suckers with scattered amplexicaul scales, tunics of fine-textured fibres. *Stem* erect, flexed outwards above sheath of fourth leaf, simple or with one or rarely more branches, 0.8–1.2 mm diam. below spike. *Cataphylls* pale and membranous, uppermost dark green or dry. *Leaves* usually 5–7, sometimes more, lower three to four basal, lower three usually reaching to at least base of spike or exceeding it; blades linear, (1–)2–4 mm wide, rigid, midrib thickened and raised, margins sometimes lightly thickened, cauline leaves shorter than basal, uppermost without a blade and sheathing for most of its

length, lower margins free almost to base. Spike inclined, lightly flexuouse, 8-17-flowered; bracts cream-coloured or pale grey-green, flushed pinkish above, dry and pale near apices, the outer (14-)17-21 mm long, acute, the inner two thirds to almost as long as outer, acute or lightly notched. Flowers white or cream-coloured to pale salmon-pink, tepals each with a narrow, dark red, longitudinal median streak, often lacking or incomplete on dorsal tepal, lower tepals sometimes with yellow streak in centre, unscented; perianth tube (22–)25–35 mm long, cylindrical below for 20-30 mm, curved and weakly flared in upper 5-6 mm, much exceeding bracts; tepals unequal, all narrowed below into claws and more or less spade-shaped, attenuate and with twisted and undulate tail-like tips, dorsal largest, inclined over stamens, arching upward near apex, $25-35 \times 8-11$ mm, claw ± 5 mm, upper laterals directed forward, arching outward in upper half, $19-25 \times 4.0-4.5$ mm, claw ± 7 mm, windowed between bases of dorsal and upper lateral tepals, lower three tepals joined to upper laterals for 1.5–3.0 mm and to one another for 2.5-4.0 mm, with small thickened knobs at sinuses between lower tepals, free parts 15–18 \times 1.5 mm, narrowed below into channelled claws 3–4 mm long, abruptly flexed downward into a narrowly lanceolate limb, in profile lower tepals exceeding upper. Filaments 10–12 mm long, exserted 6–8 mm from tube; anthers 5.0-6.5 mm long, dull blue; pollen creamcoloured. Ovary oblong, 3.5-4.5 mm long; style arching over stamens, dividing between middle and apices of anthers, branches, 1.5-2.0 mm long. Capsules ovoidellipsoid, 12×7 mm. Seeds ovate, 6.5×4.0 mm, translucent light brown, seed body dark brown, large in relation to the wing. Chromosome number: unknown. Flowering time: March to April. Figure 3.

Distribution and biology: Gladiolus sekukuniensis is known from two sites in Sekukuniland, west of the Transvaal Drakensberg (Figure 2). It grows in open woodland on the Strydpoortberge and nearby Leolo Mountains overlooking the upper Olifants River Valley. In both localities the species grows on alkaline soils. On the Strydpoortberge it occurs among Acacia caffra and Combretum molle on banded ironstone in soil containing lumps of calcrete associated with the surrounding dolomite, while on the Leolo range it occurs on norite with Kirkia wilmsii and Catha transvaalensis (another Sekukuniland endemic). Non-flowering plants are difficult to see among the tufts of Themeda triandra with which they are often associated. In form and colouring the flowers of G. sekukuniensis are highly reminiscent of those of G. macneilii Oberm. (section Densiflorus: series Calcaratus), a local edaphic endemic restricted to adjacent dolomite hills where the Olifants River cuts through the Transvaal Drakensberg. This species is known to be pollinated by the long-proboscid fly Stenobasipteron wiedemannii (Nemestrinidae) (Goldblatt & Manning 1998, 1999). The flowers of G. sekukuniensis conform to this pollination syndrome in morphology and flowering time and are apparently adapted to pollination by the same or another long-proboscid fly species. Several species of Gladiolus endemic to the Wolkberg centre of endemism in the highlands of Mpumalanga and Northern Province are adapted to pollination by long-proboscid flies in the family Nemestrinidae and these flies are clearly an important factor

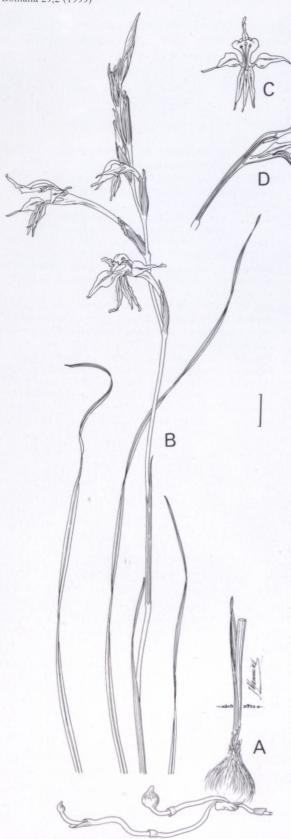


FIGURE 3.—Gladiolus sekukuniensis P.J.D.Winter. A, corm with cataphylls; B, flowering spike and leaves; C, flower, front view; D, half-flower. Scale bar: 10 mm. Artist: John Manning.

in the floral diversification of the genus there. The majority of these plants are grassland species which are visited by the fly *Prosoeca ganglbaurii*, but a few, including *G. macneilii*, *G. saxatilis* Goldblatt & J.C. Manning and *G. sekukuniensis* favour more wooded savanna or forest margin habitats and are probably all pollinated by *Stenobasipteron wiedemannii*.

History: first reported in 1997 from the Leolo Mountains by Sylvia Thompson of Haenertsburg, Gladiolus sekukuniensis was then collected from the Bewaarkloof area in the southern foothills of the Strydpoortberge in 1999, and subsequently from the population on the Leolo Mountains. Mervyn Lötter, a botanist with Mpumalanga Parks Board, has also reported the species from the same general area, bringing the number of known populations to three.

Diagnosis and relationships: the narrowly linear leaves without conspicuously thickened margins or evident secondary veins and the distinctively windowed flowers (in profile gaping between the dorsal and upper lateral tepals) with the tepal apices conspicuously tailed, indicate a very close relationship between G. sekukuniensis and G. permeabilis subsp. edulis (Burch. ex Ker Gawl.) Oberm. (section Hebea, series Permeabilis). Although widespread throughout southern Africa, G. permeabilis does not appear to have been recorded from Sekukuniland itself. It occurs on a variety of soil types, from deep Kalahari sands to fine-grained doleritic clays, but apparently not on dolomitic or other alkaline soils. The two species can be distinguished on details of flower colour and markings and in the length of the perianth tube. In addition, the suckers commonly produced from the base of the corm in G. sekukuniensis are unknown in G. permeabilis. The flowers of G. permeabilis subsp. edulis vary from a pale yellowish cream colour to dull purple, the lower tepals usually each with a narrow median yellow marking outlined with purple, and the perianth tube is obliquely funnel-shaped, shorter than the dorsal tepal and 9-15 mm long. The flowers of G. sekukuniensis are white or cream-coloured to pale salmon pink, each of the tepals with a median dark red streak, and the perianth tube is cylindrical, longer than the dorsal tepal and 22-35 mm long.

The species may also be confused with *G. macneilii* on account of the general resemblance in floral form between the two, but the flowers of *G. macneilii* are not windowed in profile because the tepals are not clawed, the upper lateral tepals are not marked, the perianth tube is rather longer, 40–45 mm long, and the anthers are distinctly tailed at the base.

G. sekukuniensis can be accommodated in the keys in the recent monograph Gladiolus in southern Africa (Goldblatt & Manning 1998) by inserting the following couplets into the key to section Hebea at lead 29 (p. 55) and into the key to Gladiolus in Botswana, northern Namibia, the northern provinces of South Africa and Swaziland at lead 21 (p. 59) respectively.

- 29' Perianth tube longer than dorsal tepal, (22-)26-35 mm long

- 21 Perianth windowed in profile (gaping between dorsal and upper lateral tepals); tepals with ribbon-like apices; flowers cream-coloured or pale pink to mauve with dark median streaks or markings on lower or all tepals, unscented or sweetly scented

Material examined

NORTHERN PROVINCE.—2429 (Zebediela): Bewaarkloof, Farm Hooggenoeg 293 KS, southeast shoulder of small plateau, 700 m south of Island Blue Waterfall, 1 200 m, 21 Mar. 1999, (-BB), *P.J.D. Winter 3232*. 2430 (Pilgrim's Rest): Steelpoort, Sekukuniland, Leolo Mountain foothills, Farm Dsjate 249 KT, 800 m east of Motse River, 1 000 m, 3 Apr. 1999, (-CA), *P.J.D. Winter 3283* (NBG, holo.; K, MO, NBG, PRE, UNIN).

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