

The genus *Solanum* (Solanaceae) in southern Africa: subgenus *Leptostemonum*, section *Giganteiformia*

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ABSTRACT

In the genus *Solanum* L. (Solanaceae), subgenus *Leptostemonum* (Dunal) Bitter, section *Giganteiformia* (Bitter) Child has four representatives in the *Flora of southern Africa* region (South Africa, Namibia, Botswana, Swaziland, Lesotho), namely *S. giganteum* Jacq., *S. goetzei* Dammer, *S. tettense* Klotzsch var. *renschii* (Vatke) A.E. Gonçalves and *S. tettense* Klotzsch var. *tettense*. Descriptions, discussions, distribution maps and keys are presented, as well as an illustration of *S. goetzei*.

INTRODUCTION

In the genus *Solanum* L., the prickly subgenus *Leptostemonum* (Dunal) Bitter is represented by eight sections in southern Africa. Three sections (*Giganteiformia*, *Melongena*, *Oliganthes*) contain only indigenous taxa, and the remaining five sections (*Acanthophora*, *Androceras*, *Cryptocarpum*, *Leprophora*, *Torva*) have only introduced species. Section *Giganteiformia* (Bitter) Child is represented by four taxa in southern Africa; all are indigenous. *S. giganteum* Jacq. occurs from tropical Africa (also India and Sri Lanka) to the Western Cape, *S. goetzei* Dammer grows from Kenya to northern KwaZulu-Natal, while *S. tettense* is found from tropical Africa to Namibia, Botswana and the northern provinces of South Africa. Detailed descriptions and discussions are given for both the section and all four taxa, together with keys and distribution maps. *S. goetzei* is illustrated for the first time. Information on distribution, ecology, phenology and uses came from specimens in NH and PRE, unless otherwise stated.

DESCRIPTIONS AND DISCUSSIONS

Section *Giganteiformia* (Bitter) Child in Feddes Repertorium 109, 5 & 6: 415, 416 (1998). Lectotype species: *S. giganteum* Jacq. (Child 1998).

Series *Giganteiformia* Bitter: 255 (1921).

Description (based on Child 1998)

Medium-sized shrubs to small trees 2–6 m high, white-pubescent to tomentose-floccose with sessile to shortly stipitate stellate hairs (also some simple hairs), stellate hairs transparent and hyaline, often small, sometimes sparse. *Prickles* short, 2–6 mm long, ± absent to many rosoid on stems, smaller on midribs, broad-based, recurved, laterally compressed, often sparse, sometimes absent or replaced with bristles. *Sympodial units* pluri-foliolate with inflorescence remaining erect for some time, especially on early order shoot generations (then branching dichasial); leaves and extended inflorescences often

aggregated terminally. *Leaves* broadly ovate to obovate, oblanceolate or ovate-lanceolate, petiolate (10–40 mm long), usually unarmed, entire to subrepand, rarely lobed, tip acute to acuminate or obtuse, basally acute or rounded, to at least 250 mm long on vigorous vegetative shoots, herbaceous, glabrescent above, white or canescently pubescent to tomentose below. *Inflorescence* cymose (in southern Africa) with few to many (20–80) dense, small, all bisexual flowers; peduncle 20–40 mm long, terminal and suberect until finally pushed laterally by continued shoot growth, sometimes armed with small deltoid/rosoid prickles; pedicels 15–18 mm long, nutant at anthesis, ± erect in fruit. *Calyx* campanulate, lobes broadly ovate or deltoid. *Corolla* stellate, mostly less than 20 mm diam., mostly blue/purple, usually deeply divided, 4-, 5- or 6-lobed, lobes narrowly triangular or linear-lanceolate. *Stamens*: filaments free; anthers equal, subleptostemonoid, lanceolate, ± attenuate. *Ovary* crowned with shortly stipitate floor glands or few stellate hairs; style glabrous. *Fruits* globose, held ± erect, 6–12 mm diam., juicy, bitter, shiny, red to purplish when ripe. *Seeds* reticulate, 2.0–2.5 mm long, pale yellow. *Chromosome number*: $n = 12$ for *S. giganteum* (Bukanya-Ziraba 1996).

Distribution and ecology

Section *Giganteiformia* consists of ± nine species in Africa, India and Sri Lanka. All these species are indigenous to Africa; only one species, *S. giganteum*, also occurs in India and Sri Lanka. Members of this section are centred in tropical East Africa from Ethiopia to Tanzania, but outlying species are found in tropical West Africa and temperate South Africa. They grow in grassland, savanna, forests and forest clearings and edges.

Taxonomy and relationships

In the subgenus *Leptostemonum* the plants are generally prickly at least when young; hairs, at least some of them, are truly stellate; inflorescences are extra-axillary; anthers are tapering, opening by terminal pores.

Bitter (1921) placed his series *Giganteiformia*, containing Afro-Asian species, with the neotropical species in section *Torva* Nees. Later authors realized that section *Torva* should not include these Afro-Asian plants.

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Whalen (1984) separated the *Giganteum* group. He observed that this group of African species is unusual in containing some species with plurifoliate and others with difoliate sympodia. The difoliate species tend to have smaller inflorescences and sometimes tetramerous flowers. However, many other distinctive characters unify the group, among them the entire, often markedly discoloured leaves with glabrate upper surfaces and closely spaced, upwardly arching lateral veins; the small broad-based prickles (often sparse); the inflorescence branches with closely spaced small, pendent flowers; the tendency to floral tetramery; and the small, juicy, erect red berries. Jaeger & Hepper (1986) kept them together in section *Torva* for convenience, but emphasized the differences between the neotropical, mainly Central American, species of section *Torva* (lobate leaves, bifoliate geminate sympodial units, white flowers and firmer, larger, green to yellow fruits) and the African species of that section. Thus, they concluded, *Solanum torvum* Sw. and *S. giganteum* Jacq. should not be in the same section.

Child (1998) noted that the appearance of his section *Giganteiformia* closely resembles that of species of section *Brevantherum* (of the subgenus *Brevantherum*) in branching pattern, in the attitude of the flowering and fruiting inflorescence and in leaf form. However, Child (1979) also noted that most species in section *Giganteiformia* are prickly, unlike section *Brevantherum*, but on the other hand, some species have a thick stellate indumentum like species of section *Brevantherum*. (Section *Brevantherum* has pleiochasial, multilateral corymbose to subumbellate cymes with a long common axis or peduncle but with reduced rachides. The inflorescence remains erect and shoot continuation is delayed until well after anthesis.) Bitter (1921) noticed that the pseudostipular leaves in the axils of cauline leaves in *Solanum giganteum* are similar to those of *S. mauritianum* and some other species of section *Brevantherum*.

Species of section *Giganteiformia* may therefore be regarded as parallel to the section *Brevantherum*, at least in respect of branching pattern and habit. According to Child (1998), plurifoliate sympodial units with ditrichasial branching, lanceolate or ovate unlobed leaves and pleiochasial inflorescences may be regarded as pleiomorphic characters within the genus *Solanum*.

Levin *et al.* (2006) concluded that most of the Old World species of subgenus *Leptostemonum* belong to a single species-rich clade. Their investigations of *Solanum kwebense* (from tropical and southern Africa) and *S. schimperianum* (from tropical Africa) suggest that within their large Old World clade, the *S. giganteum* group appears monophyletic.

Key to species of section *Giganteiformia* in southern Africa (based on Gonçalves 2005)

- 1a Leaves ± glabrous below at maturity; prickles absent; inflorescence a branched cyme; seeds 3–5 × 2.5–4.0 mm ... *S. goetzei*
- 1b Leaves markedly hairy below at maturity; prickles mostly present; inflorescence an unbranched or paniculiform cyme; seeds 2.5–3.8 × 2–3 mm:
 - 2a Leaves white floccose-tomentose below; anthers 2–4 mm long *S. giganteum*
 - 2b Leaves grey- or yellow-tomentose below; anthers 4–7 mm long *S. tettense*

1. *Solanum giganteum* Jacq., *Collectanea austriaca ad botanicum* 4: 125 (1791); Jacq.: 11, t. 328 (1793); Dunal: 258 (1852); Wright: 94 (1904); Wright: 229 (1906); Bitter: 256 (1921); Compton: 516 (1966); Palmer & Pitman: 1984 (1973); Symon: 117, t. 37 (1981); Whalen: 215, fig. 10 (1984); Beentje: 580 (1994); Van Wyk & Van Wyk: 118 (1997); Gonçalves: 88 (2005). Type: cultivated in Hortus Vindobonensis, Vienna, originally from the Cape, South Africa (Gonçalves 2005).

S. niveum Vahl ex Thunb.: 36 (1794). Type: from Cape of Good Hope, South Africa (Gonçalves 2005).

S. farinosum Wall. ex Roxb.: 255 (1824). Type: from India (Wright 1904).

Description (based on Gonçalves 2005)

Short-lived, soft-wooded, much-branched undershrub, shrub or sometimes a small tree, up to 6 m high; sympodia plurifoliate. *Hairs* stellate, white, very fine, floccose, ± sessile, regular, with many short rays. *Prickles* stout, straight or slightly curved, ± flat and triangular, 1–5 mm long, often white hairy in lower half. *Branches* white-tomentose, prickles scattered, sometimes quite unarmed, sometimes ± glabrescent. *Leaves* usually closely set at ends of branches, evergreen, rarely drought deciduous; petiole white-tomentose, 10–85 mm long; stem leaves sometimes bearing 1 or 2 leaf-like, elliptic to obovate pseudostipules at base, 10–40 × 5–20 mm; lamina membranous, elliptic to broadly ovate, obovate, lanceolate or oblanceolate, 50–250 × 20–100 mm, apex usually ± acuminate, base cuneate to sub-rounded, narrowing to petiole and ± unequal-sided, softly textured, markedly discoloured, at first velvety whitish silver-tomentose on both surfaces, soon glabrescent and dark green shiny above, persistently tomentose and rarely with 1 or 2 short prickles beneath, with 9–12 pairs of closely pinnate lateral nerves; margin entire or ± repand-sinuate. *Cymes* terminal or subterminal, becoming lateral, 45–100 mm long, corymbiform to ± paniculiform, dense, 20 to > 60-flowered, densely white-tomentose, sometimes ± glabrescent in fruit; peduncle 15–45 mm long; flowers and fruit often found on same plant, even in one inflorescence. *Flowers* faintly scented, (4)5(6)-merous, ± nodding; pedicels 5–20 mm long, slender, reflexed in flower, in fruit elongated up to 25 mm, ± thickened, erect. *Calyx* 4–6 mm long, campanulate or cyathiform, in fruit saucer-shaped, densely white-tomentose outside, unarmed, ± accrescent; lobes lanceolate-triangular to deltate or ovate-triangular, 1–4 × 1–2 mm, obtuse or acute, sometimes ± acuminate. *Corolla* mauve to blue or purple, rarely white, midvein of each lobe green, rotate; limb 10–16 mm across; lobes lanceolate to oblong, 5–7 mm long, acute to acuminate, tomentose outside, few stellate hairs on midvein and near apex inside, widely spreading to reflexed. *Stamens* yellow; filaments ± 0.5 mm long; anthers 2–4 mm long, linear or lanceolate-elliptic in outline, with small terminal pores, ± incurved. *Ovary* ± globose, ± 1 mm diam., mostly glabrous; style 5–8 mm long, exceeding stamens, straight or ± curved at apex, mostly glabrous. *Fruits* often numerous, ± globose, 5–10 mm diam., smooth, glossy, green ripening through orange to bright red, finally purplish red. *Seeds* numerous, compressed, obliquely reniform to suborbicular in outline, 2.5–3.8 × 2–3 mm, shallowly reticulate, straw-coloured to ± whitish. *Chromosome number*: 2n = 24 (Bukunya-Ziraba 1996).

Taxonomy and diagnostic characters

Solanum giganteum shows some resemblance to the invasive shrub, *S. mauritianum* Scop., which is a native of South America and a Declared Weed in South Africa (Henderson 2001). However, that species has no prickles, has yellow fruit and is very densely velvety or felty hairy in almost all parts. Gonçalves (2005) stated that in *S. giganteum* the very fine snow-white tomentum on the underside of the leaves (tending to become greyish or yellowish in old herbarium specimens), contrasting with the almost glabrous upper surface, is highly distinctive.

Distribution

Solanum giganteum is a widespread, mainly Afro-montane species that has a disjunct distribution in Africa south of the Sahara from Nigeria and Cameroon in the west to Ethiopia in the northeast and down to the Cape Peninsula (Gbile 1979). In southern Africa it has been recorded in Swaziland and South Africa where it occurs in all provinces except the Free State and Northern Cape (Figure 1). It also grows in southern India and Sri Lanka (Deb 1979). Gonçalves (2005) reported that *S. giganteum* is widespread throughout tropical and southern Africa, usually as a highland species, recorded from Ethiopia southwards throughout East Africa to South Africa (Western Cape) and westwards to Nigeria, Cameroon and Gabon, extending to the Canary Islands (Tenerife).

Africa can be divided into 18 major phytochoria according to White's system (1976); *Solanum giganteum* is widespread mainly in the Afromontane Archipelago-like centre of endemism in western, eastern and southern Africa.

Ecology

In southern Africa *Solanum giganteum* usually grows in dense to partial shade in forests, forest margins, undergrowth and clearings, among trees and often on river banks, in ravines and other moist places. It is common in high rainfall areas, up to 2 000 mm annual rainfall and is a component of woodland and grassland at a wide range of altitudes from 5–2 000 m. It can grow on steep or gentle slopes of all aspects and prefers humus-rich, well-drained brown or red sandy or loamy soils, also stony soils. The geology has been described as granite, Swaziland rocks, middle Ecca sandstone. The flowering time is in summer from October to April. Fruiting specimens have been collected throughout the year, but mainly from December to July; fruit remain on the plant for at least six months. Larger birds such as bulbuls, doves and loeries feed on the fruit, particularly in late winter when food is in short supply. It can also occur as a weed in disturbed areas. Wells *et al.* (1986) listed *S. giganteum* as an occasional ruderal or silvicultural weed that grows in dry to moist soil, in temperate to subtropical areas with summer, winter or all year rainfall. In the *Flora zambesiaca* area, it grows in forest edges, riverine forest and among rocks on granite outcrops; from sea level to 1 650 m (Gonçalves 2005).

Medicinal and horticultural uses

Pappe (1850) reported that the application of the woolly lower surface of the leaves of *Solanum giganteum* (*S. niveum*) to festering ulcers 'cleanses them, and a

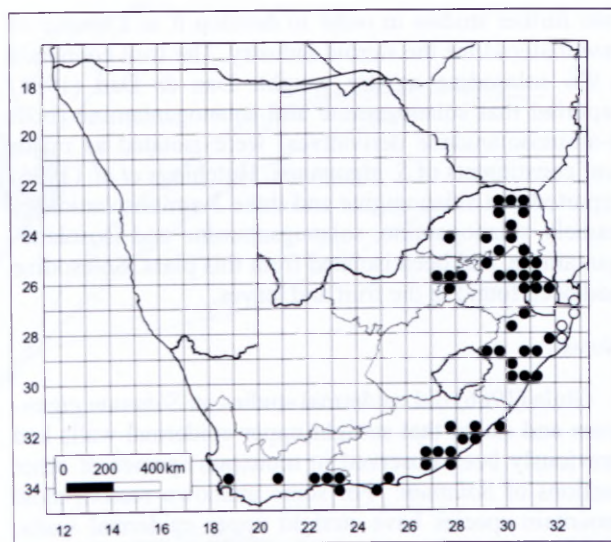


FIGURE 1.—Distribution of *Solanum giganteum*, ●; and *S. goetzei*, ○, in the FSA region.

cure is afterwards effected by applying the upper surface. Hence the Dutch name *Geneesblaren*. The fresh juice of the berries and leaves, when formed into an ointment with lard or fat, is also in use amongst the farmers for the same purpose'. Watt & Breyer-Brandwijk (1962) noted that the Xhosa and Mfengu in the Eastern Cape use the berry to curdle milk. The berry has also been used as a remedy for throat abscesses. Doses of the fresh immature and mature fruit have produced no ill effect in the rabbit. Various parts of the plant have given negative tests for saponin. Fox & Norwood-Young (1982) had a report from Modjadje's Reserve in Duiwelskloof, Limpopo Province, that the berry of this plant is used to curdle milk, and also that the 'red bitter apple' is considered edible. The fruit is used for throat ulcers by the Zulu, Xhosa and Mfengu; the fruit also curdles milk. The leaves are used for festering sores, either directly applied as a dressing or used in ointments (Hutchings *et al.* 1996).

The fruits and leaves of *Solanum giganteum* are used in traditional medicine in Uganda. The leaves are used for the treatment of insomnia and the leaves and fruits for ulcers (Bukonya-Ziraba 1996).

Solanum giganteum is often seen in botanical gardens, especially in the northern hemisphere. It is cultivated in gardens and parks in South Africa and elsewhere as an attractive ornamental shrub or small tree with shiny dark green leaves and showy bright red fruit. It forms a spectacular subtropical bedding plant. It can be used as a background plant in herbaceous borders and also as part of a hedge (Nichols 2002). Seeds germinate easily when cleaned out of the fruit. Seedlings grow rapidly and the plant should be fruiting in the second year. Bailey & Bailey (1977) listed it as a garden subject for southern California. Symon (1981) reported that it is occasionally grown in gardens in Australia, but is not known to be naturalized. In English-speaking countries it is known as African holly.

Chemotaxonomy and chemistry

Maiti *et al.* (1979) found that *Solanum giganteum* contained sufficient quantities of total alkaloids to war-

rant further studies in order to develop it as a source of raw material for the steroid industry. The fruit contained 1.9% solasodine as dry weight. Dan & Dan (1984) reported that solanogantine and solanogantamine (both 3-aminosolanidane derivatives) were isolated as major leaf constituents of *S. giganteum*. Hutchings *et al.* (1996) reported that solanogigine and three 3-aminosolanidanes namely solanogantine, solanogantamine and isosolanogantamine, had been isolated from this plant. Solasodine had been found in the fruit and leaves.

Notes

Gbile (1986) did epidermal studies on *Solanum giganteum* and stated that straight upper epidermal walls had previously been observed in mountain species of other sections of *Solanum*: 'For some unknown reason, most mountain species have straight upper epidermal walls. Some workers, however, observed that straight-walled epidermal cells are commoner in xeromorphic plants than in mesomorphic ones, which typically have undulate cell walls'.

Gbile & Sowunmi (1979) described the pollen of *Solanum giganteum* from Nigeria as subprolate and triangular, polar axis $\pm 30 \mu\text{m}$, equatorial diameter $\pm 25 \mu\text{m}$, with the exine pattern faintly distinct.

Solanum giganteum appears on the official Tree Lists of South Africa (no. 669.4) and Zimbabwe (no. 1014). Various common names for this species have been recorded in southern Africa e.g. healing-leaf tree, *geneesblaarboom* (Afrikaans), *icuba lasendle* (Xhosa). Gonçalves (2005) listed red bitter apple or red bitter berry for the *Flora zambesiaca* area.

2. *Solanum goetzei* Dammer, Botanische Jahrbücher 28: 473 (1901); Wright: 218 (1906); Bitter: 269 (1921); Jaeger: 352 (1985); Beentje: 580 (1994); Gonçalves: 91 (2005). Types: syntypes from Tanzania (Gonçalves 2005).

S. muha Dammer: 186 (1906). Type: syntypes from Tanzania (Gonçalves 2005).

Description (based on Gonçalves 2005)

Erect, much-branched perennial herb or shrublet, rarely scandent, up to 2 m high; prickles absent; sympodia difoliate; hairs stellate, whitish, sometimes violaceous or reddish tinged, minute, \pm sessile, regular, with many short rays. Branches terete, floccose-tomentose at first, gradually glabrescent. Leaves solitary or partly subgeminat; petiole 5–45 mm long, base purple; lamina thin, soft, membranous, lanceolate to obovate, 30–225 \times 10–90 mm, apex acute or acuminate, rarely \pm obtuse, base cuneate, gradually narrowing into the petiole and \pm unequal-sided, somewhat subrepand to scarcely undulate, rarely \pm entire, tending to dry blackish, initially with \pm abundant whitish hairs, soon becoming sparsely hairy to quite glabrous with age, dark green above, underside paler, with 5–9 pairs of lateral nerves. Cymes soon leaf-opposed or leaf-remote, forked 1 or 2 times or rarely unbranched, racemiform, 15–30 mm long, 3–24-flowered, \pm pulverulent-tomentose; peduncle 1–18 mm long; densely stellate-tomentose, rhachis 1–8 mm long. Flowers (4)5-merous, \pm nodding, unscented; pedicels 5–11 mm long, slender, purple, often at first densely hairy,

glabrescent, except at base, in fruit elongated to 16 mm, somewhat thickened distally, ascending or erect. Calyx 2–5 mm long, somewhat accrescent, campanulate or cupular, \pm hairy; 5-lobed, lobes \pm unequal, ovate-triangular to triangular-elongate or broadly obovate, 0.5–3.0 \times 0.5–1.0 mm, acute or mucronate to narrowly long-acuminate, in fruit enlarged to 5 \times 2 mm, finally \pm reflexed. Corolla bluish to pale violet or lilac, sometimes white, campanulate-stelliform; limb 8–15 mm across; deeply 5-lobed, lobes \pm lanceolate, 3–8 \times 1.0–3.5 mm, acute, \pm densely hairy outside mainly on median part, glabrous except for a few stellate hairs scattered along midvein or only near apex inside, erect to reflexed. Stamens 5, subequal; filaments glabrous, 0.5–1.0 mm long; anthers lanceolate-elliptic in outline, 3–5 \times 0.8–1.2 mm, slightly obtuse, \pm emarginate at apex, yellow. Ovary \pm globose, 0.7–1.0 mm diam., glabrous or with few minute glands near apex; style 4.5–8.5 mm long, glabrous, exceeding stamens, often arcuate at apex, glabrous or with few minute glands near base, white; stigma subglobose, green. Fruit globose, 6–10 mm diam., green, shining bright to deep red when ripe, soft. Seeds few, compressed, somewhat obliquely reniform, 3–5 \times 2.5–4.0 mm, surface reticulate-tuberculate, pale yellowish. Chromosome number: unknown. Figure 2.

Taxonomy and diagnostic characters

Solanum goetzei is closely related to *S. schumanianum* Dammer from the upland forests of Kenya and Tanzania and also to *S. anomalum* from West Africa. This is the species which Ross (1972) referred to as *Solanum* sp. no. 30 (Ward 3840) from Tongaland. The shrubby, unarmed habit and thin, soft, dark green, glabrescent lanceolate to obovate leaves as well as the very large seeds of *S. goetzei* are unique among the species of *Solanum* found in southern Africa.

Distribution

This species has been recorded from Kenya, Tanzania, Malawi and Mozambique down to the Ingwavuma, Ubombo and Hlabisa (Tongaland) Districts of KwaZulu-Natal (Figure 1). According to White's system (1976), *Solanum goetzei* is endemic to the Zanzibar-Inhambane and Tongaland-Pondoland regional mosaics; these form an intermittent strip of forest along the east coast of Africa.

Ecology

Whalen (1984) observed that his *Giganteum* group is divided between montane forest and savanna habitats in Africa. The species with difoliate sympodia (e.g. *Solanum goetzei*) are probably derived within the group and occupy open savannas, grasslands and forest margins. According to Jaeger (1985), this species grows in disturbed or open places in the forests of East Africa between a few metres above sea level and 1 200 m altitude. Beentje (1994) reported that *S. goetzei* grows in forest, riverine forest and coastal bushland in Kenya. In the *Flora zambesiaca* area, Gonçalves (2005) reported that this species grows in dry forest margins and the understorey, *Combretum-Terminalia* and mopane woodland, savanna woodland and coastal bushland, sometimes on termite mounds or around granite outcrops, ruderal places and other areas of disturbance, particularly along



FIGURE 2.—*Solanum goetzei*, A–D, M.C. Ward 1328 (PRE); C.J. Ward 3840 (PRE). A, habit, $\times 1$; B, flower, $\times 3$; C, fruit, $\times 1.5$; D, seed, $\times 1.5$.
Artist: G. Condy.

roads. In South Africa it grows on well-drained sandy soil at forest margins, in clearings and along forest paths, also in woodland, in deep as well as light shade, from about sea level to 100 m altitude. In KwaZulu-Natal, flowering and fruiting material have been collected from November to May.

Medicinal and other uses

Dammer (1901) cited Goetze who wrote that the roots are used as medicine against toothache. Magogo & Glover 1030 (PRE) from Tanzania noted that 'a hot poultice made from the leaves is used to reduce swellings and to draw out abscesses; also used to draw out whitlows on the fingers'. Jaeger (1985) stated that *Solanum goetzei* is

used as a leaf vegetable in Kenya, while Beentje (1994) noted that, also in Kenya, a poultice of the leaves is used to draw out abscesses.

Toxicity and chemistry

The chemistry and toxicity, if any, of this plant have not yet been investigated.

3. *Solanum tettense* Klotzsch in Peters, Naturwissenschaftliche Reise nach Mossambique, Botanik 6,1: 237 (1861); Dammer: 355 (1895); Wright: 212 (1906); Bitter: 276 (1921); Gonçalves: 86 (1997); Gonçalves: 92 (2005). Type: Mozambique, Tete Prov., Tete ('Tette'), *W. Peters s.n.* (B, holo.; BM, K, iso.) [Gonçalves 1997].

Description (based on Gonçalves 1997)

Erect, semi-woody herb or shrub, laxly to much branched from base, sometimes scrambling, up to 3 m high; covered with grey to yellowish/brownish dense tomentum of \pm sessile, short-radiate, stellate hairs, or bearing a long central ray, sometimes apically glandular, minute to large hairs all over (at least when young), and also of simple, apically glandular, spreading hairs sparsely intermixed, then pruinose, finally glabrous on some parts; prickles few to many, laterally compressed, broad-based, straight or curved, \pm stout, pale yellow to brown, 1–5 mm long, stellate-tomentose in lower half or glabrous, sometimes absent; sympodia difoliate. *Stems* and *branches* \pm terete, glabrescent, bark smooth to \pm rough, pale yellow/brown-grey to dark grey, sometimes with conspicuous lenticels. *Leaves* solitary or appearing geminate, sometimes closely set at terminals; petiole 4–40 mm long, densely to \pm hairy, prickles usually absent; lamina membranous, papery, leathery or \pm fleshy, \pm discoloured, obovate to lanceolate, 15–140 \times 5–80 mm, apex obtuse-rounded to \pm acuminate, base rounded to cuneate, narrowing into the petiole, \pm unequal, with 4–7 pairs of curved-ascending lateral nerves, greyish/yellowish below, tomentose to subglabrescent; green above, stellate-hairy to glabrescent; rarely 1–few prickles on midrib; margins repand-sinuate to entire. *Inflorescences* terminal, cymes becoming lateral, unbranched to several times forked, 30–50 mm across, few to many-flowered, often dense; peduncle 0–30 mm long; rachis 7–45 mm long. *Flowers* 4 or 5(–7)-merous, \pm nodding; pedicels 3–13 mm long, elongated in fruit, up to 18 mm long, \pm thickened distally, erect. *Calyx* greyish/yellowish, densely to \pm hairy outside, 2.5–6.0 \times 3–6 mm, \pm accrescent, campanulate or cupular; lobes lanceolate to broadly obovate, 1.0–3.5 \times 1–2 mm, apically rounded, long-acuminate, 5 \times 2 mm in fruit, \pm reflexed, glabrous inside. *Corolla* white to mauve, blue, violet or purple, 6–13 mm long, \pm rotate; limb 6–22 mm across, lobes oblong-ovate to linear, 4–11 \times 1.5–4.5 mm, apex acute/obtuse, greyish or whitish hairy outside, mainly on median part, mostly glabrous inside, erect to reflexed. *Stamens* \pm equal, glabrous, exerted; filaments 0–1.5 mm long, whitish; anthers yellow to orange-yellow, 4–7 mm long, \pm lanceolate in outline, opening by 2 small, oblique pores. *Ovary* globose/ellipsoid, 1.0–1.5 mm diam./length, glabrous; style 5–11 mm long, slender, longer than stamens, straight or \pm apically curved, glabrous; stigma small, capitate, obtuse or slightly 2-lobed. *Fruits* globose, 5–10 mm diam., green turning yellow-brown to deep red when ripe, fleshy, glossy, glabrous, in axillary clusters or pseudo-terminal cymes. *Seeds* numerous, compressed, obliquely reniform, reticulate-tuberculate, 3.0–3.5 \times 2–3 mm, \pm pale yellow, drying blackish. *Chromosome number*: $2n = 24$ (Bukonya-Ziraba 1996).

Key to varieties (from Gonçalves 1997)

- Stellate hairs often bearing a long central ray intermixed with simple, long, spreading, \pm abundant hairs, both apically glandular. var. *tettense*
 Stellate hairs eglandular, sometimes intermixed with simple, short, abundant, apically glandular hairs var. *renschii*

3a. var. *tettense*

See description above.

3b. var. *renschii* (Vatke) A.E. Gonç. in *Kirkia* 16,1: 89, fig. 1 (1997); Gonçalves: 93, t. 18 (2005). Type: Kenya, Central Prov., Machakos or Kitui Dist., Ukamba (Ukambani area), J.M. Hildebrandt 2735 (B, holo.; W, iso.) [Gonçalves 1997].

S. renschii Vatke: 328 (1882). Type: as above.

S. kwebense N.E.Br. ex C.H. Wright: 225 (1906). Types: Botswana, Ngamiland, Kwebe Hills, Lugard 50 (K, lectosyn.), Mrs Lugard 62 (K, syn.) [Gonçalves 1997].

S. luederitzii Schinz: 264 (1912). Type: Namibia, Hereroland, Lüderitz 1a [Podlech & Roessler 1969].

S. upingtoniae Schinz: 266 (1912). Type: Namibia, Amboland, Os-hando, Schinz 868 [Podlech & Roessler 1969].

S. tenuiramosum Dammer: 244 (1912). Type: Botswana, Masalanyane Pan (Massaringani Vlei), Seiner II.271 (B, holo.) [Gonçalves 1997].

S. chondropetalum Dammer: 335 (1915). Type: Namibia, Damaraland, Naugubais, Dinter 1448 [Podlech & Roessler 1969].

Taxonomy and diagnostic characters

Wright (1906) and Bitter (1921) recognized *Solanum kwebense*, *S. renschii* and *S. tettense* as three distinct species. Lebrun & Stork (1997) recognized both *S. kwebense* and *S. renschii* (*S. tettense*), whereas Podlech & Roessler (1969) recognized only *S. kwebense*. Studies by Gonçalves (1997) revealed that both the vegetative and inflorescence characters of these three species show a strong intergradation. Therefore these taxa constitute a single polymorphic species with great morphological and ecological diversity. *S. tettense* is the correct name for this species. The two varieties cannot be separated on geographical or ecological terms.

The diagnostic characters of *Solanum tettense* in relation to the other two members of section *Giganteiformia* in southern Africa, are outlined in the key above. *S. tettense* can be distinguished from other *Solanum* species in the same area by its pedunculate cymes and entire, discoloured leaves without prickles.

Gonçalves (2005) observed that *Solanum tettense* is somewhat intermediate between section *Giganteiformia* and section *Oliganthes*; it is relatively common in the *Flora zambesiaca* area, but is easily overlooked or misidentified.

Distribution

Solanum tettense is widespread throughout tropical and southern Africa; it is recorded from Ethiopia southward through East Africa to South Africa, and westward to Zaire, Angola, Botswana and Namibia. In southern Africa, var. *renschii* is found in Namibia, Botswana and the Limpopo and Mpumalanga Provinces in South Africa (Figure 3). In southern Africa var. *tettense* occurs only in Botswana (Figure 3). According to White's system (1976), *S. tettense* is widespread in the Somalia-Masai regional centre of endemism, but is also found in the Zambezi regional centre of endemism and in the Kalahari-Highland regional transition zone.

Ecology

In southern Africa, *Solanum tettense* grows on well-drained red or brown, shallow to deep, dry to damp, sandy or loamy soils that can be stony or quartzitic. It is often found on weathered granite, gneiss or dolomite outcrops and inselbergs, also on calcified dolomite or calcrete soils. This species grows on flat areas such as the edges of pans or on flood plains, but also on moderate or steep slopes of all aspects, on sandy dunes and rocky hillsides. It has been collected on termitaria, in disturbed and overgrazed areas, also on roadsides. *S. tettense* grows in full sun but more often in the semi-shade or shade of taller shrubs or trees, also in dense thickets. Larger leaves develop in shady habitats. It becomes invasive in overgrazed vegetation with a reduced grass cover.

Solanum tettense grows in vegetation types ranging from grassland and savanna to various kinds of deciduous or evergreen woodland and bushland. Trees and shrubs such as *Acacia*, *Boscia*, *Combretum* and *Grewia* are commonly associated with *S. tettense*.

The rainfall in the distribution area of *Solanum tettense* var. *renschii* in southern Africa, is 400–1 000 mm per year and it grows at an altitude of 335–1 370 m. *Flowering time*: October to March, mainly from January to March. *Fruiting time*: November to May, mainly from January to April.

Gonçalves (2005) stated that in the *Flora zambesica* area, including Botswana, *Solanum tettense* grows in mixed woodland, mopane and wooded grassland or thickets, extending into miombo on termite mounds, also streamsides, rocky places and areas of disturbance in moist and semi-arid situations at 100–1 600 m altitude.

Medicinal and other uses

Maguire noted on the label of his specimen *B. Maguire 2272* in PRE (collected at Karakuwise in Namibia in 1953), that the fruits provide ingredients for the arrow poison of the Khoi-San (Bushmen). Barnard noted on the label of his specimen *Barnard 153* in

PRE (collected in Sekhukhuneland near Lydenburg in Mpumalanga Province in November 1934), that 'the roots are cooked and placed in a calabash (fruit of *Lagenaria siceraria*), in which a small opening has been made. The calabash is then fastened over a suppurating wound to draw out the pus'. Collectors have noted that *Solanum tettense* is eaten by the large antelope, the eland. The Tswana common name *mwarasupe* is listed by Miller on the label of his specimen *B/469* in PRE, collected in Botswana. The Kamba in Kenya use the roots against typhoid (Beentje 1994).

Toxicity

Pienaar *et al.* (1976) proved that *Solanum tettense* can be poisonous to cattle. A neurological disease of cattle (named *maldronksiekte* by farmers), occurring in a localized, badly overgrazed area of the Limpopo Province of South Africa, was experimentally reproduced at Onderstepoort Veterinary Institute by feeding *S. tettense* var. *renschii* plants (known as *rooibessie* among farmers) to cattle. According to Vahrmeijer (1981), the disease is characterized by temporary loss of balance and transient epilepsy-like seizures precipitated by a variety of stimuli, such as exercise, handling (dipping and loading) and fright. The animal staggers about with an extended and slightly twisted neck, and in serious cases falls to the ground. After a while it rises again as if nothing were wrong. Losses are suffered when animals are injured during falls. When not disturbed, most affected animals appear to be completely normal. The poison affects the central nervous system and causes permanent damage to, and interferes with the function of the cerebellum. *Maldronksiekte* is a chronic intoxication with a latent period of at least 50 days between ingestion of the plant and the appearance of typical clinical signs. Donkeys, goats and sheep are apparently not affected by the poison. The chemistry of *S. tettense* var. *renschii* was not investigated in the above study.

SPECIMENS EXAMINED (southern Africa only)

Specimens held at PRE, unless otherwise indicated. The numbers in brackets indicate the identity of the specimens: (1) *Solanum giganteum*; (2) *S. goetzei*; (3a) *S. tettense* var. *tettense*; (3b) *S. tettense* var. *renschii*.

Abner 71 (3b). *Acocks 11519* (1). *Acocks & Hafström 1376* (3b). *Allen 346* (3b). *Ankiewicz 8* (2).

Barnard 153, 529 (3b). *Barnard & Mogg 857, 1013* (1); *1082* (3b). *Bayliss 1132, 7052* (1). *Brink 294* (1). *Bruce 46* (3b). *Burger 1020* (3b). *Buitendag 1162* (1) Lowveld Botanical Garden, PRE. *Burgoyne 3076, 3423, 3241* (3b).

Codd 5921 (1); *4147, 5984, 8884* (3b). *Coetzee 1154* (1). *Compton 25550, 30071* (1). *Crampton 113* (1). *Curson 465, 481, 526* (3b).

Davidse 6814 (1). *Devenish 1580* (1). *De Winter 2817* (3b); *8273* (1). *De Winter & Leistner 5095, 5516* (3b). *Dinter 5312, 7448* (3b). *Dlamini s.n. PRE31390* (1).

Edwards 1318 (1).

Flanagan 472 (1).

Galpin 2854, 7815, 9039 (1). *Germishuizen 7540, 7765, 9552, 9770* (3b). *Gerstner 5747* (1); *6047* (3b). *Giess 9277, 12592, 15016* (3b). *Giess & Müller 11808, 13977* (3b). *Giess, Watt & Snyman 11129* (3b). *Giffen 1086, 1437* (1). *Goldblatt & Manning 8399* (1).

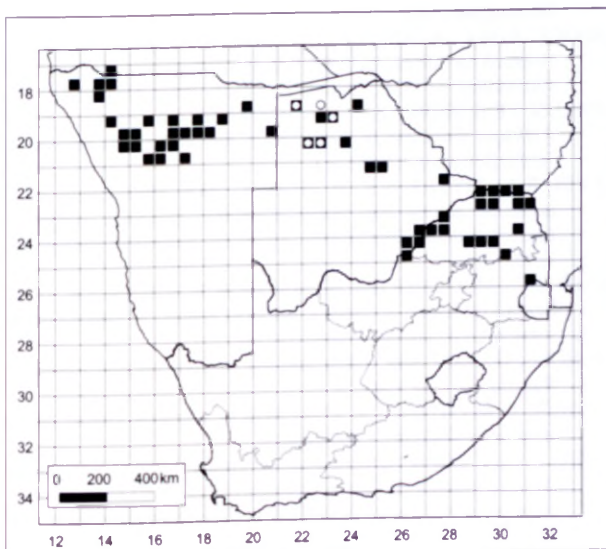


FIGURE 3.—Distribution of *Solanum tettense* var. *tettense*, ○, and var. *renschii*, ■, in the FSA region.

Hansen 3355 (3b). Harbor TRV14089 (3b). Hardy, Retief & Herman 5363 (1). Haynes 967a (1). Hemm 597 (1). Henning 5 (3b). Hilner 475 (1). Hines 638 (3b). Holt 135 (1). Hobohm PRE41601 (3b). Hoffmann LH204 (3b). Hulley, Olckers & Hill 379 (3b). Huntley 1049 (3b); 1306 (1).

Jacobsen 729, 2906 (1); 2200 (3b). Junod 4291 (1).

Kerfoot & Falconer 41, 156 (3b). Killick 401, 1707 (1). Kluge 718 (1) Lowveld Botanical Garden, PRE. Kotze 84 (3b).

Lawson 324, 340 (2) NH. Leendertz 554, 689 (1). Leistner 3160 (3b). Leistner, Oliver, Steenkamp & Vorster 41 (3b). Lent 46 (3a). Le Roux 819 (3b). Liebenberg 2950 (1); 4821, 4918 (3b). Louw 15 (1).

MacDevette 883 (2) NH. Maguire 2272 (3b). Mannheimer & Mannheimer CM530 (3b). Marloth 4311, 5677 (1). Marriott PRE22643 (1). Meeuse 10457 (3b). Merxmüller & Giess 30455 (3b). Meyer 1031 (1). Müller B/469, B/1197 (3b). Mogg 11511, 12455, 15004, 36077 (1). Moll & Morris 693 (1). Morris 711 (1). Moss 2085 (3b). Morze 2085 (1). Müller & Biegel 2302 (3b). Muller & Scheepers 225 (1). Munro TRV23163 (1).

Naude 1/94 (3b). Nienaber EN325 (1).

Obermeyer TRV28143, TRV29223 (1). Obermeyer, Schweickerdt & Verdoorn 57 (3b). Onderstall 916 (1) Lowveld Botanical Garden, PRE.

Paterson TRV25847 (1). Pegler 709, 2890 (1). Pentz 299 (1). Pienaar 367 (3b). Pole Evans 238 (1); 1933, 4536 (3b). Pott PRE59768 (1). Prior PRE41307 (1).

Raal 809, 1388 (3b). Repton 621, 1005 (1). Rodin 3959, 4519 (1). Rogers PRE3791, 14455, 23467 (1).

Scheepers 676 (1). Schoenfelder 1004 (3b). Sim 1272, 20000, 20006 (1). Smith 357A, 6868 (1); 3101 (3b). Stalmans 555 (1). Stephens 7 (1). Story 6481 (3b). Straub 158 (3b). Strey 3477 (3b); 3843 (1); 4786 (2) NH, PRE.

Theron 1511 (1); 2879 (3b). Thode A1292 (1). Thorncroft TRV3930 (1). Tölken & Hardy 894 (3b).

Van der Schijff 3503 (3b); 4600, 4874, 7357 (1). Van der Spuy 10 (3b). Van Rooyen 3401 (3b). Van Son TRV29022 (3b). Van Vuuren 89 (1). Van Warmelo 275 (3b). Van Wyk 3681 (1). Van Wyk & Van Wyk 1599 (1). Venter 3795 (1); 12820 (3b). Volk 966, 2911 (3b).

Wahl TRV15368 (1). Ward 87, 399, 1328 (2) NH; 608, 2961 (1); 3226, 3840, 7053 (2). Watt & Breyer-Brandwijk 1027 (1). Welman 432 (1). Westfall 1009 (1). Wild & Drummond 6857 (3a).

Zwanziger 758 (3b).

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REFERENCES

- BAILEY, L.H. & BAILEY, E.Z. 1977. *Hortus third, a concise dictionary of plants cultivated in the United States and Canada*. Macmillan, New York.
- BEENTJE, H.J. 1994. *Kenya trees, shrubs and lianas*. National Museums of Kenya, Nairobi.
- BITTER, G. 1921. *Solana africana* III. *Botanische Jahrbücher* 57: 248–286.
- BUKENYA-ZIRABA, Z.R. 1996. Uses, chromosome number and distribution of *Solanum* species in Uganda. In L.J.G. van der Maesen, X.M. van der Burgt & J.M. van Medenbach de Rooy, *The biodiversity of African plants*: 33–37. Kluwer Academic Publishers, Dordrecht.
- CHILD, A. 1979. A review of branching patterns in the Solanaceae. In J.G. Hawkes, R.N. Lester & A.D. Skelding, *The biology*

and taxonomy of the Solanaceae: 345–356. Linnean Society of London.

- CHILD, A. 1998. Studies in *Solanum* and related genera (6). New infra-generic taxa for the genus *Solanum* L. (Solanaceae). *Feddes Repertorium* 109, 5,6: 407–427.
- COMPTON, R.H. 1966. An annotated checklist of the flora of Swaziland. *Journal of South African Botany*, Supplement no. 6.
- DAMMER, U. 1895. Solanaceae. In H.G.A. Engler, *Pflanzenwelt Ost-Afrikas und der Nachbargebiete*, Teil C: 351–356. Reimer, Berlin.
- DAMMER, U. 1901. Berichte über die botanischen Ergebnisse der Nyassa-See- und Kinga-Gebirgs-Expedition. *Botanische Jahrbücher* 28: 473–477.
- DAMMER, U. 1906. Solanaceae africanae I. *Botanische Jahrbücher* 38: 176–195.
- DAMMER, U. 1912. Solanaceae africanae II. *Botanische Jahrbücher* 48: 224–260.
- DAMMER, U. 1915. Solanaceae africanae III. *Botanische Jahrbücher* 53: 325–357.
- DAN, S. & DAN, S.S. 1984. Chemotaxonomy of the genus *Solanum*. *Journal of Economic and Taxonomic Botany* 5: 875–879.
- DEB, D.B. 1979. Solanaceae in India. In J.G. Hawkes, R.N. Lester & A.D. Skelding, *The biology and taxonomy of the Solanaceae*: 87–112. Linnean Society of London.
- DUNAL, M.F. 1852. Solanaceae. In A.P. de Candolle, *Prodromus systematis naturalis regni vegetabilis* 13: 1–690. Masson, Paris.
- FOX, F.W. & NORWOOD-YOUNG, M.E. 1982. *Food from the wild. Edible wild plants of southern Africa*. Delta, Johannesburg.
- GBILE, Z.O. 1979. *Solanum* in Nigeria. In J.G. Hawkes, R.N. Lester & A.D. Skelding, *The biology and taxonomy of the Solanaceae*: 113–120. Linnean Society of London.
- GBILE, Z.O. 1986. Epidermal studies in the *Solanum nigrum* complex in Nigeria. In W.G. D'Arcy, *Solanaceae: biology and systematics*: 159–168. Columbia University Press, New York.
- GBILE, Z.O. & SOWUNMI, M.A. 1979. The pollen morphology of Nigerian *Solanum* species. In J.G. Hawkes, R.N. Lester & A.D. Skelding, *The biology and taxonomy of the Solanaceae*: 335–342. Linnean Society of London.
- GONÇALVES, A.E. 1997. *Solanum tettense* Klotzsch s.l. (Solanaceae) in the *Flora zambesiaca* area. *Kirkia* 16,1: 85–94.
- GONÇALVES, A.E. 2005. Solanaceae. In G.V. Pope, R.M. Polhill & E.S. Martins, *Flora zambesiaca*, vol. 8,4.
- HENDERSON, L. 2001. *Alien weeds and invasive plants*. Plant Protection Research Institute Handbook No. 12. Agricultural Research Council, Pretoria.
- HUTCHINGS, A., SCOTT, A.H., LEWIS, G. & CUNNINGHAM, A.B. 1996. *Zulu medicinal plants, an inventory*. University of Natal Press, Pietermaritzburg.
- JACQUIN, N.J. VON. 1791. *Collectanea austriaca ad botanicum, chemiam et historiam naturalem spectantia, cum figuris* 4. Kraus, Vienna.
- JACQUIN, N.J. VON. 1793. *Icones plantarum rariorum* 2. Wappler, Vienna.
- JAEGER, P.-M.L. 1985. *Systematic studies in the genus Solanum in Africa*: 1–540. Unpublished Ph.D. thesis, University of Birmingham, UK.
- JAEGER, P.-M.L. & HEPPER, F.N. 1986. A review of the genus *Solanum* in Africa. In W.G. D'Arcy, *Solanaceae, biology and systematics*: 41–55. Columbia University Press, New York.
- LEBRUN, J.P. & STORK, A.L. 1997. *Énumération des plantes à fleurs d'Afrique tropicale IV*. Solanaceae: 386–400. Conservatoire et Jardin Botaniques, Genève.
- LEVIN, R.A., MYERS, N.R. & BOHS, L. 2006. Phylogenetic relationships among the 'spiny solanums' (*Solanum* subgenus *Leptostemonum*, Solanaceae). *American Journal of Botany* 93, 1: 157–169.
- MAITI, P.C., MOOKHERJEA, S., MATHEW, R. & DAN, S.S. 1979. Studies on Indian *Solanum* I. Alkaloid content and detection of solasodine. *Economic Botany* 33: 75–77.
- NICHOLS, G. 2002. Add colour and life to your hedges. *Farmer's Weekly*, Grow 10 May: 13.
- PALMER, E. & PITMAN, N. 1973. *Trees of southern Africa*, vol. 3 (new edn). Balkema, Cape Town.
- PAPPE, L. 1850. *Florae capensis medicae prodromus: or an enumeration of the South African indigenous plants used as remedies by colonists of the Cape of Good Hope*. Robertson, Cape Town.
- PETERS, W.C.H. 1861. *Naturwissenschaftliche Reise nach Mossambique*, *Botanik*, vol. 6,1. Reimer Berlin.
- PIENAAR, J.G., KELLERMAN, T.S., BASSON, P.A., JENKINS, W.L. & VAHRMEIJER, J. 1976. *Maldronksiekte in cattle: a neu-*

- ronopathy caused by *Solanum kwebense* N.E.Br. *Onderstepoort Journal of veterinary Research* 43,2: 67–74.
- PODLECH, D. & ROESSLER, H. 1969. Solanaceae. In H. Merxmüller, *Prodromus einer Flora von Südwestafrika* 124: 1–17. Cramer, Weiheim.
- ROSS, J.H. 1972. The flora of Natal. *Memoirs of the Botanical Survey of South Africa* No. 39.
- ROXBURGH, W. 1824. *Flora indica*. In W. Carey & N. Wallich, *Descriptions of Indian plants, by the late William Roxburgh*, vol. 2, edn 1. Serampore, India.
- SCHINZ, H. 1912. Beiträge zur Kenntnis der Afrikanischen Flora. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich* 56: 229–268.
- SYMON, D.E. 1981. A revision of the genus *Solanum* in Australia. *Journal of the Adelaide Botanic Garden* 4: 1–367.
- THUNBERG, C.P. 1794. *Prodromus plantarum capensium* 1. Edman, Uppsala.
- VAHRMEIJER, J. 1981. *Poisonous plants of southern Africa that cause stock losses*. Tafelberg, Cape Town.
- VAN WYK, A.E. (Braam) & VAN WYK, P. 1997. *Field guide to trees of southern Africa*. Struik, Cape Town.
- VATKE, G.C.W. 1882. Plantas in itinere africano ab J.M. Hildebrandt collectas determinare pergit. *Linnaea* 43: 324–334.
- WATT, J.M. & BREYER-BRANDWIJK, M.-G. 1962. *Medicinal and poisonous plants of southern and eastern Africa*, edn 2. Livingstone, Edinburgh and London.
- WELLS, M.J., BALSINHAS, A.A., JOFFE, H., ENGELBRECHT, V.M., HARDING, G.G. & STIRTON, C.H. 1986. A catalogue of problem plants in southern Africa. *Memoirs of the Botanical Survey of South Africa* No. 53: 483–491.
- WHALEN, M.D. 1984. Conspectus of species groups in *Solanum* subgenus *Leptostemonum*. *Gentes Herbarum* 12,4: 179–282.
- WHITE, F. 1976. The vegetation map of Africa—the history of a completed project. *Boissiera* 24b: 659–666.
- WRIGHT, C.H. 1904. Solanaceae. In W.T. Thiselton-Dyer, *Flora capensis* 4,2: 87–121.
- WRIGHT, C.H. 1906. Solanaceae. In W.T. Thiselton-Dyer, *Flora of tropical Africa* 4,2: 207–261.