

The genus *Solanum* (Solanaceae) in southern Africa: subgenus *Leptostemonum*, the introduced sections *Acanthophora* and *Torva*

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ABSTRACT

In the genus *Solanum* L. (Solanaceae), subgenus *Leptostemonum* (Dunal) Bitter, section *Acanthophora* Dunal has four representatives in the *Flora of southern Africa* region (South Africa, Lesotho, Swaziland, Namibia, Botswana), namely *S. aculeatissimum* Jacq., *S. capsicoides* Allioni, *S. mammosum* L. (cultivated only) and *S. viarum* Dunal. Section *Torva* Nees has two representatives in southern Africa, namely *S. chrysotrichum* Schldl. (*S. hispidum* auct. non Pers.) and *S. torvum* Sw.; both are naturalized weeds. *Solanum capsicoides*, *S. viarum* and *S. torvum* have not been listed before for southern Africa. All are introduced species native to the New World. Descriptions, discussions, illustrations and distribution maps of the naturalized species are presented, as well as keys to the species of both sections.

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Detailed descriptions and discussions are given for both sections and all six species, together with keys, illustrations and distribution maps. *S. mammosum*, being cultivated only, has no distribution map.

DESCRIPTIONS AND DISCUSSIONS

Section ***Acanthophora*** Dunal, *Histoire naturelle, médicale et économique des Solanum*: 131, 218 (1813). Lectotype species: *S. mammosum* L. (D'Arcy 1972).

Section ***Aculeata*** G. Don subsection *Acanthophora* (Dunal) G. Don: 434 (1838).

Psilocarpa, grad. ambig., Dunal: 216 (1852).

Section ***Simplicipilum*** Bitter: 147 (1923). Lectotype species: *S. aculeatissimum* Jacq. (Seithe 1962).

Description (based on Nee 1991)

In the genus *Solanum* L., the prickly subgenus *Leptostemonum* (Dunal) Bitter is represented by eight sections in southern Africa. Two sections contain only indigenous taxa, one section contains mainly indigenous taxa, and the remaining sections have only introduced species. Section *Acanthophora* Dunal is represented by four species in southern Africa. All are originally from the Americas, namely the rather common and widespread weed *S. aculeatissimum*, the relatively rare weed *S. capsicoides*, the cultivated ornamental *S. mammosum*, and *S. viarum* which is becoming a fairly common weed in KwaZulu-Natal and neighbouring areas. *S. capsicoides* and *S. viarum* have not been listed before for southern Africa (Welman 1993). Section *Torva* Nees is represented by two species in southern Africa; both are originally from the Americas. *S. chrysotrichum* is so far naturalized only in Eastern Cape, while *S. torvum* is confined to a fairly small area north of Durban, KwaZulu-Natal.

Small shrubs, 0.3–3.0 m tall, sprawling or more often erect and few-branched, annuals or short-lived perennials, heavily armed with straight acicular (needle-shaped) prickles, in some species stems with additional robust recurved prickles from enlarged compressed bases. *Stems* usually glandular-puberulent, often also eglandular-pilose with few-celled, simple hairs. *Leaves* petiolate, alternate or usually geminate, with one about twice the size of the other; blades usually ovate to orbicular and with 2–4 pairs of lobes, or repand, coarsely and irregularly toothed, membranous, spiny along main veins above and below, usually glandular-puberulent above and usually also eglandular-pilose with simple few-celled hairs, these sometimes with vestigial rays at base, below with simple hairs and sessile few-rayed stellate hairs (these lacking in *S. capsicoides*). *Inflorescences* lateral, simple or few-branched, sessile or shortly pedunculate, remote from leaves, axis often spiny; flowers few to many, fewer than half fertile, often only lowest fertile in large-fruited species. *Calyx* seldom much accrescent; lobes triangular to linear. *Corolla* white, yellowish, green-

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ish or blue-purple, glandular and pilose on outside, stellate, without interstitial pleating. *Ovary* glabrous or minutely stipitate-glandular, puberulent in few species with simple hairs that drop off early. *Fruit* usually globose, small to large, strongly dark green and pale green marbled when young, yellowish, orange or reddish at maturity, glabrous at maturity, exocarp \pm tough, mesocarp juicy, in some species becoming dry at full maturity, placentae simply columnar, divided or variously intruded, the fruit becoming effectively or completely unilocular at maturity. *Seeds* numerous, subreniform to orbicular, seed coat closely investing endosperm or extending around periphery of seed into a flattened wing.

Distribution and ecology

According to Whalen (1984), section *Acanthophora* occurs throughout the American tropics except in Amazonian Brazil; it is most diverse in the northern Andes and in southeastern Brazil. About 20 species grow in open savanna and disturbed sites. Several species are established in the Old World tropics.

Nee (1979) noted that this section, in common with almost all groups of *Solanum*, has great weedy tendencies; the species are found in areas of high light intensities and also where the natural vegetation has been disturbed. Under natural circumstances, landslides, eroded stream banks and forest openings provide suitable habitats. Man's agricultural and industrial practices are still expanding the ranges of numerous species of *Solanum*. The succulent berries of many species are popular with birds and ensure seed dispersal.

Taxonomy

Dunal (1813) appropriately named this group of prickly species section *Acanthophora* (thorn-bearing). In 1923, Bitter referred to the characteristic hairs of this section in the name *Simplicipilum*. However, Dunal's name for this section must take precedence.

In 1972, D'Arcy elevated subsection *Lasiocarpum* Dunal of section *Acanthophora* to section *Lasiocarpum* (Dunal) D'Arcy, with *S. lasiocarpum* Dunal as type species. Section *Acanthophora* can be distinguished from section *Lasiocarpum* by the lack of stellate hairs on the ovaries, the more general coverage with multi-celled simple hairs and the less substantial habit (Jaeger 1985). Section *Lasiocarpum* is indigenous to South America and no representatives have so far been recorded from southern Africa, though a few species are naturalized and/or cultivated in East Africa; see Jaeger (1985).

Whalen (1984) placed *S. aculeatissimum*, *S. capsicoides*, *S. mammosum* and *S. viarium* in his *S. mammosum* Group.

Microscope studies

Section *Acanthophora* has distinctive simple hairs that are long, multicelled, uniseriate, shiny and translucent. These simple hairs are identical with the central ray of the stellate hairs on the same plant; the latter often

only present on juvenile plants or leaves. During evolution the basal side rays of the stellate hairs have apparently disappeared. Single-celled simple hairs, often gland-tipped, may also occur on the upper surface of the leaf as well as elsewhere on the plant (Nee 1979).

Diagnostic characters

According to Whalen (1984), the *S. mammosum* Group of species is distinguished by an essentially herbaceous habit, difoliate-geminate sympodia, vestiture of predominantly simple hairs, variously lobed or dentate, prickly leaves, lateral, often simple inflorescences, stelliform corollas and dryish, glabrous berries.

Nee (1979) stated that section *Acanthophora*, as a member of the prickly subgenus *Leptostemonum* (Dunal) Bitter, deserves its name; all the species are heavily armed with sharp, slender prickles and some species have stouter, broad-based prickles as well. He defined the section by the combination of the upper leaf surface bearing only simple hairs, glabrous fruit and the non- to only slightly accrescent calyx.

This section can be divided into two subsections based on the seed morphology (Nee 1979). One subsection, with seeds that do not differ much from those of almost all other *Solanum* species, includes *S. aculeatissimum*, *S. mammosum* and *S. viarium*. The other subsection is characterized by seeds surrounded by a broad, flattened margin or wing, a character unique in *Solanum*. This subsection is probably monophyletic and includes *S. capsicoides*. The evolutionary significance of the winged seed is not clear; it could aid in wind or water dispersal.

Sex forms and branching

Whalen & Costich (1986) described section *Acanthophora* as weakly to strongly andromonoecious; having both perfect and male flowers, but no female flowers. Species of this section have some short-styled flowers, and are self-compatible. The fruits are small to large; it was found that andromonoecy in section *Acanthophora* is most strongly developed in large-fruited species.

Child (1979) and Child & Lester (1991) studied the branching patterns in the Solanaceae. All sections of the subgenus *Leptostemonum* have 2- or 3-foliate sympodial units often with the subtending leaf paired with the smaller first leaf of the daughter shoot (anisophyllous geminate sympodia). Section *Acanthophora* has mostly simple few-flowered inflorescences with only the basalmost flower and/or the few proximal flowers of the subsidiary inflorescence hermaphrodite; the distal flowers are usually smaller, brachystylous or short-styled (andromonoecious; Symon 1979) and are often inserted with a spatial gap from the hermaphrodite flowers. Species with prickly calyces in the hermaphrodite flowers usually have unarmed, functionally male, brachystylous flowers.

Note

Nee (1991) noted that this section contains a number of promising candidates for screening for alkaloids.

Key to species of section *Acanthophora* in southern Africa (from Jaeger 1985)

- 1a Seeds 4–6 mm diam., prominently winged; branches and leaves almost glabrous to sparsely hairy; ripe fruit vermilion (sometimes cultivated) *S. capsicoides*
- 1b Seeds 2–5 mm diam., not winged; branches and lower leaf surface hairy; ripe fruit yellow:
- 2a Stems with acicular prickles only; branches with scattered simple hairs *S. aculeatissimum*
- 2b Stems prickly with both compressed and recurved and long, straight acicular prickles; branches hirsute with dense, simple hairs:
- 3a Hairs on stem of variable lengths, 2–4 mm long; calyx not prickly; corolla violet; fruit globose, usually with an apical nipple and several basal protuberances; seeds 5 mm diam. (cultivated only) *S. mammosum*
- 3b Hairs on stem of uniform lengths, up to 5 mm long; calyx prickly; corolla white; fruit globose; seeds \pm 2 mm diam *S. viarium*

1. *Solanum aculeatissimum* Jacq., *Collectanea austria ad botanicum* 1: 100 (1787a); Jacq.: t. 41 (1787b); Bitter: 148 (1923); Heine: 334 (1963); Pearse: 173 (1978); Gbile: 115 (1979); Jaeger: 478 (1985); Bukenya & Hall: 84 (1988); Nee: 265 (1991); Bukenya & Carasco: 51 (1995); Retief & P.P.J. Herman: 622 (1997); Shaw: 234, 239 (2000). Type: cultivated plant at Vienna, 'Patria in zona torrida est', *Jacquin s.n.* (W).

S. reflexum Schrank: t. 81 (1822). Type: cultivated plant in Hortus Monacensis (Munich), *von Schrank s.n.* (M).

S. khasianum C.B. Clarke: 234 (1883). Type: India, Khasia Mts, Nunklow, *J.D. Hooker & T. Thomson 14* (CAL).

S. cavaleriei L veill  & Vaniot: 207 (1908). Type: from China, *J. Cavalerie 2722* (E).

Annual, sparsely branched herb or undershrub up to 1.5 m high, pubescence highly variable, dense to sparse (plant rarely nearly glabrous). *Stems* tinged purple and green, rarely densely pubescent, with simple, uniseriate, multicellular hairs of unequal lengths, up to 4 mm long, heavily armed with many slender, acicular, straight, spreading or slightly reflexed prickles up to 12 mm long with base 0.5 mm broad. *Leaves* ovate, up to 160 \times 180 mm, base truncate or slightly cordate, lobation variable, usually doubly or dentately lobed to $\frac{1}{3}$ width of leaf, with 3 or 4 pairs of major acute, triangular lobes, middle lobe up to 55 mm long, dark green when fresh, usually drying dull dark green, with simple pilose hairs on both surfaces of leaves, rarely with stellate hairs on underside, prickles on midrib and petiole slender, \pm 15 mm long, base \pm 2 mm broad, prickles on primary lateral veins slender, \pm 7 mm long, purple near base, upper part yellow, the base 0.8 mm broad; petiole 4–80 mm long. *Inflorescences* simple, 3–5(6)-flowered; peduncles up to 0.5 mm long; pedicels \pm 10 mm long. *Calyx*: lobes often unequal, elongating immediately after anthesis and concealing immature fruits with subcaudate lobe tips, pubescent, becoming prickly in fruit. *Corolla* 10–15 \times 25–30 mm, stellate, white, greenish or yellow-green, sometimes with a purple tint, rarely with purplish hairs. *Stamens*: filaments green to yellow; anthers yellow. *Style* white; pistil pale green. *Fruit* nodding, globose, 15–30 mm diam., smooth, pale green with medium green stripes or white with green reticulation when young, dirty yellow or brownish when ripe. *Seeds* 2–4 mm

diam., brownish, moderately flattened, seed coat closely investing endosperm, with margin sometimes thickened but not wing-like. Figure 1.

Distribution

Whalen (1984) gave the distribution of this species as southeastern Brazil (natural) and Central Africa (naturalized). Jaeger (1985) stated: 'the wide distribution of this species in Africa, and its scarcity or even absence from the New World, together suggest that *S. aculeatissimum* is native to Africa. This gives section *Acanthophora* an inexplicably disjunct distribution. However, *S. aculeatissimum* grows as a weed of secondary vegetation, indicating that it is more likely to be an introduction to Africa; and when it is considered that trade routes between the New World and Africa have been established for over 400 years (Roe 1979), an early introduction of this species would allow time for its subsequent dispersal. Its hideously spiny habit must deter grazing and contribute to its success.'

Jaeger & Hepper (1986) confirmed that *S. aculeatissimum* seems to have been in Africa for a long time, having achieved a very wide distribution in the Afrotropical regions in western, eastern and southern Africa. Nee (1991) reported that *S. aculeatissimum* occurs naturally mainly from Rio Grande do Sul, Paran  and Santa Catarina states in Brazil. He also reported that this species has long been grown in European botanical gardens where it is very uniform and may represent a single introduction from South African populations, which they strongly resemble.

Because of confusion with *S. capsicoides* and other heavily armed species of *Solanum*, distribution records of *S. aculeatissimum* in the literature are often not reliable. In southern Africa, this species is fairly common in Limpopo [Northern Province], Mpumalanga, KwaZulu-Natal, Eastern Cape and rare in the Free State, Lesotho and Western Cape, with one isolated record in the North-West almost on the border with Gauteng (Figure 2). It is also sometimes cultivated as a curiosity in these areas, e.g. in botanical gardens; *Forbes NH34644* (NH) was grown at the Botanical Station, Durban in 1944.

Ecology

Nee (1991) recorded that *S. aculeatissimum* is a weedy shrub that grows in disturbed or pastured forest, in grazing fields and along roadsides, from 400–1 200 m altitude. 'In sub-Saharan Africa it is found at forest edges and in savannas, mostly in the eastern uplands of the great lakes region, but scattered through the rain forest and into South Africa, from 1 000–2 400 m, rarely descending almost to sea level.' Gbile (1979) described this as a highland species in Nigeria that grows mostly on rough ground and amongst rocks. According to Bukenya & Carasco (1995), *S. aculeatissimum* generally grows in forest clearings in Uganda; according to Bukenya & Hall (1988), it is a rare species in secondary forest in western Ghana.

In southern Africa, *S. aculeatissimum* grows in forest margins and clearings, along forest paths, and among undergrowth in closed natural forest, but also in *Pinus* and



FIGURE 1.—A, *Solanum aculeatissimum*, Acocks 10787, fruit Nienaber 9 (PRE); B, *S. torvum*, Henderson 737 (PRE). Artist: G. Condy.

Eucalyptus plantations. It prefers damp, shady places under shrubs and trees. It is also found along roadsides and in other disturbed areas, as a weed in gardens, ploughed fields as well as grassland. Wells *et al.* (1986) listed *S. aculeatissimum* as a ruderal, silvicultural and pastoral weed of the temperate and subtropical summer rainfall areas in southern Africa. It is found on gentle and steep mountain and hill slopes, in gorges and valleys, but also on flats; it can grow on moist humus-rich and red-brown loamy soil and also on well-drained sandy or stony soil. It is common in mountainous areas and is recorded from about sea level to $\pm 2\ 200$ m altitude, with a rainfall of up to 2 000 mm annually. Acocks (1988) listed *S. aculeatissimum* as one of the generally occurring smaller plants of the forest floor and margin in his Northeastern Mountain Sourveld which is one of the Inland Tropical Forest Types. He also listed it as one of the smaller plants of general occurrence in the Highland Sourveld which is one of the Temperate and Transitional Forest and Scrub Types.

Nee (1991) stated that in Brazil, its natural distribution area, flowering is confined from October to

February, similarly in East Africa, but throughout the year in the Democratic Republic of the Congo. In south-

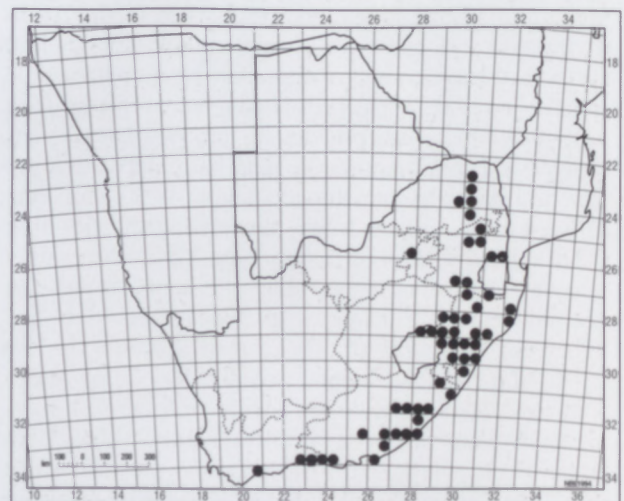


FIGURE 2.—Distribution of *Solanum aculeatissimum* in the FSA region.

ern Africa it flowers from about November to March and fruits from about November to April.

Chromosome number and chemistry

Both Fedorov (1969) and Bukenya-Ziraba (1996) listed $2n = 24$.

Dalziel (1937) reported that the stem contains solanine, an alkaloidal glucoside with physiological action like saponin, but much less poisonous. Watt & Breyer-Brandwijk (1962) also reported that *S. aculeatissimum* contains solanine. The immature fruit is said to contain more solanine than the mature. Reports that the plant is toxic to cattle, horses and even humans are suspect as they may not be referring to the true *S. aculeatissimum*. Hepper (1978) stated that the steroidal alkaloid solasodine always occurs in the fruits of *S. aculeatissimum*, but little is found in the leaves. Roddick (1986) gave figures for the amounts of solasodine in the leaves and fruit, confirming Hepper. Hutchings *et al.* (1996) reported that solasodine, solamargine and solasonine have been isolated from leaves, stems, fruit pericarps and seeds. The highest concentration of glycoalkaloids was found in seeds, followed by fruit pericarps, leaves and stems. Solasonine accounted for about 80% of the total glycoalkaloids, whereas solamargine accounted for about 13%, and was not found in stems.

Medicinal and other uses

Mehra (1979) reported that in Malaysia the leaf juice of *S. aculeatissimum* is used in a ritual preparation to be taken at childbirth. In Puerto Rico the sliced fruit of *S. aculeatissimum* (or plants known as) is fatal when consumed by cockroaches (Mabberley 1997). In Liberia, the fluid prepared by boiling the fruits of *S. aculeatissimum* is applied in an enema for constipation (Dalziel 1937). Gbile & Adesina (1988) reported the same for Nigeria. In West Africa the fruit and the root are used as remedies for cough and dysmynorrhoea.

Hutchings *et al.* (1996) reported that in Transkei, South Africa, the ripe fruit is applied to the forehead for headaches and is used for healing the navels of new-born babies, and smoke from burning plants is used for toothache (also in Nepal); root decoctions are taken for backache and impotence. An infusion of the root is a Zulu snake-bite remedy (Watt & Breyer-Brandwijk 1962). In Eastern Cape, South Africa, it was noted on the voucher, Bradley 49 (GRA), that the poisonous fruit is used for skin infections and the root for flatulence and as a purgative.

Microscope studies

Gbile & Sowunmi (1979) described the pollen of *S. aculeatissimum* as subprolate and triangular, polar axis $\pm 28.0 \mu\text{m}$, equatorial diameter $\pm 22.5 \mu\text{m}$, with the sexine pattern faintly distinct. Nee (1986) investigated the placentation pattern of *S. aculeatissimum*. The placenta is H-shaped in cross section, allowing the seeds to fill the total interior of the large fruit. At maturity the septum is a very thin film, resulting in a more or less unilocular berry. The 'ribs' running down the sides of the inner peri-

carp at the carpellary midvein strongly suggest traces of the false septum of *S. sisymbriifolium* Lam., but does not indicate a close relationship. Gbile (1986) observed straight upper epidermal walls in the leaves of *S. aculeatissimum*, which is an uncommon occurrence in a mesomorphic montane species. Groth (1989) studied the seeds of *S. aculeatissimum*; they are ellipsoid or subdiscoid with a finely punctate surface. The embryo is circinate and the cotyledons lanceolate. Ogundipe & Daramola (1997) also investigated the leaf epidermis: the anticlinal cell walls have a wavy pattern, the adaxial cells ($\pm 38.0 \times 15.5 \mu\text{m}$) have an irregular and the abaxial cells ($\pm 33 \times 15 \mu\text{m}$) an isodiametric cell shape; the abaxial stomata ($\pm 28.5 \times 17.0 \mu\text{m}$) are anomocytic.

Taxonomy and diagnostic characters

S. aculeatissimum (seeds not winged) has often been and still is confused with *S. capsicoides* (= *S. ciliatum* Lam.) (seeds winged) e.g. in Wright (1904); Wright (1906); Bailey & Bailey (1977); Mabberley (1997). D'Arcy (1972) chose *S. aculeatissimum* as the lectotype species of *Armatae* (subgenus?) and of *Macrophyllae* (section?) and of *Parviflorae* (subsection?), all of Wright (1906).

In southern Africa, *S. aculeatissimum* can be distinguished from related species by its yellow ripe fruit, seeds without wings and by its stems with scattered simple hairs and acicular prickles.

Potential for crop improvement

Several investigators have looked at hybridization with *S. melongena* L. (aubergine, brinjal, eggplant). Rao (1979) reported successful crosses between *S. melongena* and *S. aculeatissimum*. Pearce & Lester (1979) showed that *S. aculeatissimum* has very little serological relationship with the taxa of the eggplant complex. Hybrids produced seed which did not germinate. Daunay, Lester & Laterrot (1991) recorded that *S. aculeatissimum* is resistant to *Verticillium*, but susceptible to *Meloidogyne* spp., which are both eggplant pests.

Notes

The specific epithet refers to the large number of sharp prickles. Numerous common names have been recorded e.g. Bailey & Bailey (1977): cockroach berry, love apple, soda apple nightshade; Wells *et al.* (1986): apple-of-Sodom and devil's apple for southern Africa; Jeffery RUH4919 (GRA); Peru apple.

The photograph and description published by Rhind (1975) in a popular journal for South African farmers, belong to *S. aculeatissimum* and not to the indigenous *S. panduriforme* E.Mey., as claimed in the discussion accompanying the photograph.

2. *Solanum capsicoides* Allioni, Auctuarium ad synopsis methodicam stirpium horti regii Taurinensis: 64 (1773); Dunal: 156 (1852); Symon: 101, t. 29 (1981); Symon: 118, t. 26A, B (1982); Whalen: 252, t. 28 (1984); Carvalho: 77 (1985); Jaeger: 477 (1985); Troupin: 378, t.



FIGURE 3.—A, *Solanum chrysotrichum*, Stirton 6306 (PRE); B, *S. capsicoides*, Ward 4888 (PRE). Artist: G. Condy.

121.1 (1985); Bukonya & Hall: 84 (1988); Lemke: 365 (1991); Nee: 261 (1991). Type: cultivated at Turin, origin unknown, *Allioni s.n.* (TO, holo.).

S. ciliatum Lam.: 21 (1794). Type: sheet with label '*S. ciliatum* Lam. illustr. Dic. No. 55' (P-LA).

S. aculeatissimum auctt. non Jacq., C.H.Wright: 97 (1904).

S. macowanii Fourc.: 101 (1934). Type: Eastern Cape, Humansdorp Div., *Fourcade 1224* (SAM, holo.; K).

Annual or short-lived perennial, herbaceous shrub, erect to sprawling, occasionally woody at base, sometimes spreading by rhizomes, up to 1.5 m high. *Stems* green or purplish; stems, petioles, veins of upper and lower leaf surfaces, pedicels and calyces bearing scattered to many prickles, very sharp, straight, pale or straw-coloured, \pm narrowly (up to 2 mm) based, 2–14 mm long; sparsely pilose with 1.5–5.0 mm long, simple, shiny, uniseriate, few-celled hairs (stellate hairs absent) and minute, simple, glandular hairs. *Leaves* membranous or papery, concolorous green, broadly ovate in outline, up to 150 \times 135 mm, 5–7-lobed,

slightly cordate at base, sinuses reaching about halfway or less to midrib, lobes and leaf apex acute or obtuse, major

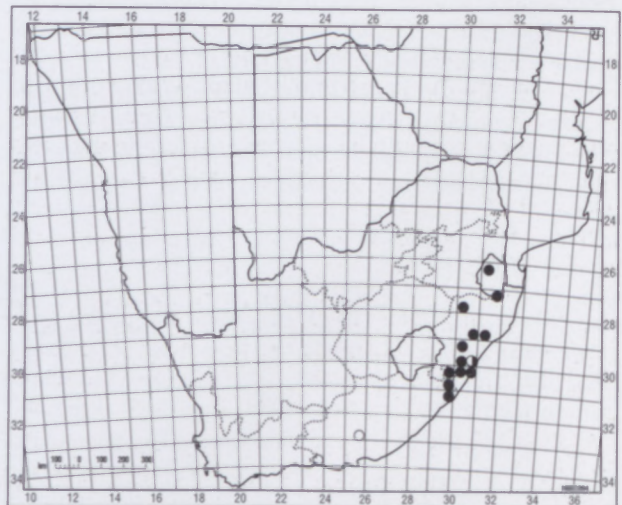


FIGURE 4.—Distribution in the FSA region, of *Solanum capsicoides*, \circ ; and *S. viarum*, \bullet ; (both species \bullet).

lobes often entire or slightly repand but scarcely pinnately lobed, margins ciliate; petiole up to 80 mm long. *Flowers* 1–7 together on short peduncle, 2–4 mm long, or pedicellate on stem in internodal position; first flowers staminate; pedicels 10–25 mm long at anthesis. *Calyx* often prickly; tube 2–5 mm long; lobes 2–5 mm long, broadly lanceolate or triangular-ovate, acute, slightly accrescent. *Corolla* 10–15 × 20–30 mm, deeply stellate with lobes ± 10 mm long, glabrous inside and outside, white or rarely pale mauve. *Stamens* subequal; filaments 1–2 mm long, glabrous; anthers 3–7 mm long, tapered upwards, erect in cone, pale yellow; pores minute; pollen 24.0–30.5 µm. *Ovary* with some glandular hairs; style 5–8 mm long, erect, pale, styles of perfect flowers exerted, those of staminate flowers equalling filaments; stigma green. *Fruit* slightly depressed-globular, 20–40 mm diam., bright, matte orange-scarlet when mature, flesh thick, white, spongy, sweetish tasting (tasteless?), dryish when ripe, containing ± 300 seeds. *Seeds* orbicular-ovoid, 4–6 mm diam., flat, minutely pitted, reticulate, area over embryo pale yellowish or light brown, bordered by a distinct, pale wing ± 1.5 mm wide. *Cotyledons* broadly ovate-lanceolate, ± 13 × 7 mm, first true leaves almost orbicular, petioles without spines, later leaves increasingly lobed. Figure 3.

Distribution

The native range is 'coastal Brazil south of the Amazon' (Nee 1979). *S. capsicoides* is adventive on the Caribbean Islands, in Central and South America, also in the southern United States. It is a common weed in southern China and elsewhere in Asia; also in New South Wales and Queensland in Australia where it is called devil's apple.

Solanum capsicoides is introduced in tropical and South Africa (probably as an ornamental) where it is so far found naturalized only around Durban in KwaZulu-Natal and in Eastern Cape (Figure 4). It was first collected in the Durban District in 1895, *J.M. Wood 5718* (K, NH). It was cultivated at the Natal Herbarium in Durban in 1933, *McClellan NH26927* (NH), and in a garden in Cape Town in 1955 (seed from KwaZulu-Natal), *Primos SAM684203* (SAM).

Ecology

Solanum capsicoides is native to coastal Brazil near Rio de Janeiro and is apparently adapted to the *restinga* vegetation of the coastal sand dunes (Nee 1979). It prefers high rainfall, coastal lowlands of tropical and subtropical regions. It becomes a naturalized weed in disturbed sites, clearings, forest margins and other open habitats. It seems to have a wide ecological range and Morton (1976) claimed that *S. capsicoides* (*S. ciliatum*) is hardy as far north as Baltimore, Maryland in the USA. Man is probably responsible for its initial wide dissemination; it has been in European botanical gardens for more than two centuries.

For some unknown reason it has spread fairly slowly in Africa. In KwaZulu-Natal it was collected at ± 15 m altitude in shade at the edge of a forest in stony sand on a disturbed site. It seems to flower and fruit throughout the year.

Chromosome number, toxic properties and potential for crop improvement

Fedorov: 695 (1969) reported $2n = 24$ (as *S. ciliatum*).

The berries were reported to be poisonous to calves in Australia (Symon 1982) and Nee (1991) noted that the fruit is considered to be poisonous in northeastern Brazil. The fruit of *S. capsicoides* is used as a cockroach poison in parts of tropical America and this plant is sometimes called cockroach berry in the United States (D'Arcy 1974). Its toxicity to humans is unknown. According to Daunay, Lester & Laterrot (1991), *S. capsicoides* is resistant to *Pseudomonas* and is a non-host plant for potato cyst-nematodes. They also reported that *S. capsicoides* is graft-compatible with *S. melongena*, but is not used as a rootstock as it contains toxic alkaloids.

Taxonomy and diagnostic characters

This species has often been confused with the quite distinct *S. aculeatissimum* which has neither winged seeds nor vermilion fruit. It was also previously known under the synonym, *S. ciliatum* (Hepper 1979). Other synonyms are listed by Lebrun & Stork (1997) and Whalen (1984). Nee (1979) believed that this species, which has been known and grown for a long time and has been described several times under various names, might have an older name which could emerge from some obscure publication. He also noted that the slightly accrescent, stoutly prickly calyx of *S. capsicoides* might indicate a relationship with *S. sisymbriifolium* Lam. of section *Cryptocarpum* Dunal.

Fourcade collected the type of his *S. macowanii* at 700 ft (± 235 m) altitude in the forest near Storms River, Humansdorp Div., Eastern Cape, in April 1921, and quoted another specimen, *MacOwan 1493*, from the Somerset East Div., also in Eastern Cape. He stated that *S. macowanii* was close to *S. acutissimum* Jacq. (*sic*) 'from which it differs by the branches and the lower surface of the leaves being glabrous, by the entire leaf lobes, and by the flowers being geminate.' Jaeger, Nee and Lester all identified the isotype of *S. macowanii* in K as *S. capsicoides*; PRE has a colour photograph of this specimen. The specimen of *MacOwan 1493* in GRA has a much more spiny stem than the type and one unripe fruit with immature seeds. Apparently *S. capsicoides* has not been collected again in Eastern Cape since 1921 and it could have died out in that area. Ross (1972) quoted *Ward 4888* as *S. aculeatissimum* Jacq. in his checklist of the *Flora of Natal*, but this specimen has orange-red ripe fruit and winged seeds and is clearly *S. capsicoides*.

The large orange-red fruit with winged seeds and the absence of stellate hairs make *S. capsicoides* unique in the southern African context.

Notes

S. capsicoides is occasionally cultivated for its ornamental vermilion dry fruits which keep their colour for a long time. [The large-fruited form common in cultiva-

tion is var. *macrocarpum* Hort. (Morton 1976).] This species could have a 'shaker' mechanism for seed dispersal (Nee 1991). The ripe dry fruit splits irregularly into 2–4 lobes and releases the dry winged seeds, which adhere neither to each other nor to the pericarp. The inner fruit wall of the unilocular ovary is \pm 4 mm thick, slightly juicy and spongy; it is nearly tasteless and dries to a virtually invisible thin film soon after the fruit begins to split. The conspicuous fruit colour could indicate a very recent derivation from ancestors with bird-dispersed seeds. Nee (1986) noted that the placentas are split into two 'horns' and at maturity are attached only to the base of the fruit. The fruit and seed dispersal method of *S. capsicoides* probably is an adaptation to its natural sandy habitat; the placentation ensures space for a great number of large seeds. The evolutionary significance of the winged seed is not clear (Nee 1979). It could perhaps aid in local dispersal by wind or water.

The species name refers to the resemblance of the fruit to that of the solanaceous genus *Capsicum*.

3. *Solanum mammosum* L., Species plantarum, edn 1: 187 (1753); Dunal: 250 (1852); D'Arcy: 712 (1973); D'Arcy: 851 (1974); Morton: 201 (1976); Bailey & Bailey: 1055 (1977); Symon: 103 (1981); Jaeger: 479 (1985); Bukenya & Hall: 83 (1988); Bukenya & Carasco: 51 (1995); Shaw: 234, 239 (2000). Lectotype: t. 226, fig. 1 in Plukenet, Phytographia, pars tertia (1692), 'Habitat in Virginia, Barbados.' Typotype: Herb. Sloane vol. 98, fol. 59 (BM); see Jaeger: 479 (1985) and Knapp & Jarvis: 342 (1990).

Annual or short-lived perennial, herbaceous shrub up to 2 m high. *Stems* and twigs white or yellow viscid-villous with 2–4 mm long simple hairs, armed with scattered yellow or green, large acicular prickles, 10–25 mm long, which with age become flattened, recurved, woody and brownish. *Stems* hollow. *Leaves* suborbicular to broadly ovate, 60–150 \times 120–200 mm, blade pinnatifid with 5–7 main broadly triangular lobes (each lobe \pm coarsely, dentately lobed), apices acute, bases truncate to cordate, sinuses rounded; both sides white- or yellow-villous, upper surface with mainly 2–4 mm long, simple glandular hairs, lower surface with sessile stellate hairs mixed with long, simple, glandular hairs; armed on principal veins on both sides with flattened, acicular prickles, 1–2 mm broad, up to 17 mm long; petioles 30–150 mm long, covered with simple hairs and some straight prickles up to 13 mm long. *Inflorescences* lateral, extra-axillary, 1–4-flowered cymes/racemes bearing both staminate and hermaphrodite flowers with only one flower fruiting per inflorescence, \pm sessile or peduncles up to 10 mm long; pedicels 5–15 mm long, becoming stout and somewhat longer in fruit, viscid-villous to lanate, sometimes armed with few small prickles. *Calyx* 8–10 mm long, deeply lobed, prickles absent; tube 2 mm long; lobes subulate-acuminate, pubescent outside. *Corolla* showy, pale blue to violet, up to 20 mm long, 40 mm wide, deeply stellate, lobes linear-lanceolate; hirsute outside, glabrous within. *Stamens* equal; filaments 1 mm long; anthers 8–12 mm long, linear-oblong, tapering with small, apical pores. *Ovary* and style glabrous. *Fruit* globose to broadly ovoid, 30–100 mm long, often with a 20 mm long nipple-like contraction at apex and 1–5 rounded protrusions at base, orange to yellow, spongy, pulp white. *Seeds* compressed-

lenticular, 5–7 mm wide, finely rugose, shiny, purple-red to dark brown, lacking marginal wing. Figure 5.

Distribution and ecology

Solanum mammosum is native to the Caribbean (Nee 1979), but has spread by long distance dispersal, direct migration or with the casual or deliberate assistance of humans to the tropical lowlands of South and Meso-America. It is now often naturalized in disturbed, lowland habitats in the tropical and subtropical regions of both hemispheres, though not yet in Africa (Jaeger 1985) or Australia (Symon 1981). Nee (1991) stated that *S. mammosum* now occurs mostly from sea level to 100 m altitude in tropical America, but can occur as high as 1 800 m. It flowers and fruits throughout the year with no special season. It can be expected to become naturalized or to escape locally from cultivation in areas of high rainfall, whether this is seasonal or year-round. It has been known as a curiosity in botanical gardens for several centuries and is occasionally cultivated as an ornamental in tropical Africa; also in southern Africa in frost-free or frost-protected localities.

Chromosome number and chemistry

Heiser (1971) gave references of reports for both $n = 12$ and $n = 11$; the latter was the first report of $n = 11$ in the genus *Solanum*. Dan & Dan (1984) recorded the occurrence of nuatigenin and iso-nuatigenin (two rare isomeric non-nitrogenous sapogenins) as the main root constituent of *S. mammosum* and some other species of *Solanum*. Roddick (1986) listed 1% of solasodine (dry weight) in the fruit of *S. mammosum*, while Mabberley (1997) referred to the molluscicidal glycoalkaloids of the fruit. Nee (1991) stated that the immature fruits contain the highest concentration of glycoalkaloids and that other plant parts contain varying amounts or none.

Medicinal and other uses, potential for crop improvement

Solanum mammosum (macaw bush, nipple fruit, pig's ears) is widely cultivated in tropical and warm temperate regions for its unique ornamental but also poisonous fruit. In the Americas, these fruits are widely used for killing rats and cockroaches, also for catching fish, extracting maggots and curing common colds (Nee 1979). Heiser (1971) quoted the use of the leaves as a narcotic in Bolivia. Daunay, Lester & Laterrot (1991) listed that *S. mammosum* is resistant to *Fusarium* wilt and several other pests and diseases of *S. melongena* cultivars. They also regarded it as frost resistant, but susceptible to *Meloidogyne incognita* and *Verticillium*, both pests of *S. melongena*.

Microscope studies

The glandular villous pubescence in this species is composed of reduced stellate hairs in which the rays are fused with the leaf lamina and the mid-point remains as an apparently simple hair (D'Arcy 1974). The structure of this hair type is best observed in seedlings. Similar hairs occur in *S. capsicoides* (= *S. ciliatum*), but they are not so dense and are less commonly glandular. Whalen & Costich (1986) listed a report on female



FIGURE 5.—A, *Solanum mammosum*, Codd 6569 (PRE); B, *S. viarum*, T. Olckers & S. Naser s.n., grown from seed collected in Brazil (Cedara Weeds Laboratory). Artist: G. Condy.

sterility of short-styled flowers in *S. mammosum*, and noted that embryo sac development in these flowers was abnormal.

Taxonomy and diagnostic characters

Whalen (1984) and Lebrun & Stork (1997) listed a number of synonyms for this species. Wright (1904) expressed doubt whether the *S. mammosum* Thunb. in his revision of the South African species of *Solanum*, is the same as *S. mammosum* L. The description does not mention the unique fruit. A specimen (*Thunberg s.n.*) collected in the Swellendam Div. (Western Cape) in the late 18th century is quoted; probably before *S. mammosum* L. was introduced into South Africa. However, no specimen of it was found in Thunberg's herbarium in 1883.

Solanum mammosum has a pubescent calyx without prickles, a showy pale blue to violet corolla, yellow,

ripe mammiform fruit and seeds at least 5 mm wide, lacking marginal wings. In southern Africa, *S. mammosum* has so far only been recorded in a cultivated state, and not yet as naturalized or even as a garden escape.

Notes on the fruit

Miller (1969) made a thorough study of the morphology and development of the unusual mammiform fruit of *S. mammosum*. Wild specimens in the Western Hemisphere show considerable variation in fruit shape, from entirely globose to mammiform with an apical nipple and five protuberances at the base. The more unusual forms were probably selected by man from a teratological abnormality and used as an ornamental and for its extremely poisonous fruit. There has apparently also been a selection for plants less prickly than the wild form (Nee 1991).

Nee (1986) studied placentation patterns in the Solanaceae. The basic fruit in *Solanum* is 2-locular with a slightly enlarged placental area in the centre of the septum, from which the seeds radiate into the usually pulp-filled locules between the septum and the pericarp. In the mature fruit of *S. mammosum*, the septum can hardly be seen, and is only a thin film, easily destroyed; the placentas are connected only at the base. Nee (1979) suggested that the spongy mesocarp may adapt the fruit to dispersal by water flotation.

4. *Solanum viarum* Dunal in DC., Prodrômus systematis naturalis regni vegetabilis 13.1: 240 (1852); Carvalho: 83 (1985); Jaeger: 482 (1985); Nee: 264 (1991); Bryson & Byrd: 382 (1994); Wunderlin et al.: 606, t. 1, 2 (1993). Type: São Paulo, Brazil, Lund 799 (G-DC, holo., -IDC microf. 2080: I.1).

S. khasianum C.B. Clarke var. *chatterjeeanum* Sen Gupta: 413 (1961). Type: Nilgiri District, Madras State, India. *K. Subramanyam 10413* (CAL, holo., iso.).

Straggling, short-lived, perennial herbs or subshrubs, 1–2 m high. *Stems* much branched at and above base; stems, petioles, pedicels and leaves densely glandular-puberulent with \pm uniform, multicelled, straight, simple hairs less than 0.5 mm long, some hairs eglandular; stem prickles few, most with thickened and flattened bases and conspicuously recurved, up to 6 mm long. *Leaves* solitary or in pairs, membranous, blades broadly ovate to ovate-triangular, base subcordate, 80–150 \times 50–150 mm, sinuate-lobed up to $\frac{1}{3}$ of way to midrib, lobes 4–6, subobtusate or subacute, lower surface also with 4 or 5-rayed stellate hairs, rays nearly always in one plane, one ray longer than rest, up to 0.5 mm long; armed on midrib and minor veins with straight, acicular, laterally compressed, broad-based, whitish to yellowish prickles up to 20 mm long; petioles 20–90 mm long, armed with similar prickles. *Inflorescences* axillary, 4- or 5-flowered; peduncles stout, 15–20 mm long. *Calyx* pubescent on outside, 4–7 mm long, 5-lobed to about middle; lobes triangular-ovate, enlarging and concealing immature fruit, then prickly on outside. *Corolla* white or greenish, 15–27 mm diam., deeply stellately 5-lobed; lobes broadly lanceolate, 8–12 mm long, recurved, apex acute to mucronate, outer surface pubescent with glandular and eglandular hairs. *Stamens* white to cream; filaments \pm 1 mm long; anthers linear-lanceolate, attenuate, 8–10 mm long, pores minute. *Ovary* globose, densely and minutely puberulent; stigma capitate. *Fruit* globose, 15–30 mm diam. when mature, minutely puberulent when young, later smooth and glabrous, immature fruit pale and dark green with white mottling, yellow at maturity with leathery skin surrounding thin-layered, pale green, mucilaginous, scented pulp. *Seeds* numerous, 190–385, moderately compressed, suborbicular, \pm 2 mm long, lacking marginal wing, surface reddish brown, very minutely rugulose, seed coat closely investing the endosperm. Figure 5.

Distribution

Originally from southern Brazil, Paraguay, Uruguay and northern Argentina, but *S. viarum* has spread to other

areas of South America, also Central America, the West Indies and the southern United States (tropical soda apple). It was introduced into India and Nepal and also into Africa; it is recorded in the Democratic Republic of the Congo and possibly also in Cameroon (Jaeger 1985). Probably accidentally and sporadically introduced into Africa and can be expected to spread to many other subtropical areas (Nee 1991).

In southern Africa, specimens have been collected in Swaziland, KwaZulu-Natal and Eastern Cape (Figure 4). The earliest record seen for this study, was collected in 1962: *Marr & Harding 54* (PRE) from the Natal Agricultural Institute, Pietermaritzburg, KwaZulu-Natal.

Ecology

Wunderlin et al. (1993) reported that in Florida *S. viarum* is usually found in soils belonging to the order of Spodosols, that means nearly level, somewhat poorly drained soils with a spodic horizon 1–2 m below ground level. In South Africa it has been collected on well-drained, reddish brown, sandy loam soil, with a western, northwestern or eastern slope, from 30–800 m in altitude; elsewhere it is reported from low altitudes, mostly below 100 m. *S. viarum* prefers full sunlight, but will also grow in the shade.

It is often a common weed of natural areas, improved pastures, croplands, roadsides and fence rows, waste places, open disturbed sites, secondary growth and forest edges. In southern Africa it was also collected in open woodland and pine plantations. In more tropical areas, flowering and fruiting occurs throughout much of the year (Nee 1991), but in southern Africa flowering and fruiting material has been collected from November to April, with one fruiting specimen in August.

Weedy characters, dispersal and control

Solanum viarum can produce up to 50 mature fruits per plant, each fruit containing numerous seeds. According to Bryson & Byrd (1994), it has been on the Florida noxious weed list since 1994. It was present in that state since about 1980 and spread very rapidly and aggressively, being able to form near monocultures in certain situations, although its opportunistic adaptations may restrict it to disturbed areas.

Its foliage is generally not grazed by cattle, probably because it is heavily armed with prickles and glandular hairs, although they will sometimes eat the bitter mature fruit. It can be transported from pasture to pasture in contaminated hay and farm machinery. The primary means of dispersal seems to be livestock and wildlife, including birds. Scarification of seeds by digestive systems of animals seems to promote seed germination. Movement of livestock that have recently fed on *S. viarum* fruit will hasten its spread. Bryson & Byrd (1994) found that in mature plants the root systems were up to 300 mm deep and lateral roots up to 1 m long. They also found that experimentally detached green fruit more than 20 mm in diameter will ripen in sunlight. Seed germination from these fruits was more than 70%. Fruit from less than 10 mm in

diameter up to mature yellow or dry fruit are extremely buoyant and can then also be dispersed by water. Control of this plant therefore requires elimination of immature and mature fruit as well as the whole plant including the root system.

Chromosome number, chemistry, medicinal use and potential for crop improvement

Fedorov (1969) gives $2n = 24$ as the chromosome number for *S. khasianum*.

The section *Acanthophora* contains several species with a high alkaloid content (Nee 1991). Of these *S. viarum* is the species most studied, as it contains a high percentage of solasodine, concentrated in the berries. Dan & Dan (1984) listed *S. viarum* as a high solasodine yielding plant (the alkaloid of pharmaceutical interest). Roddick (1986) listed 0.7–3.0% of solasodine (dry weight) in the fruit. It is a common weed in India since at least 1932 where it is also grown as a commercial source of this glycoalkaloid which is a key intermediate in the synthesis of steroid drugs (Maiti *et al.* 1979). Saini (1966) found that the 'fleshy cover' and washed seeds of *S. khasianum* var. *chatterjeeanum* do not contain any alkaloid; most is found in the mucilaginous layer around the seeds. When fruits are dried, the mucilaginous layer dries to a white powder which is easily lost or is capable of contaminating the seed or pericarp assay. This provides an explanation for the discrepancies in the literature of the glycoalkaloid content from different parts of the fruit. Daunay, Lester & Laterrot (1991) reported that *S. viarum* is resistant to the following diseases of *S. melongena*: *Leucinodes orbonalis*, *Epilachna vigintioctopunctata*, *Phomopsis* blight, 'little leaf' and partially resistant to *Meloidogyne incognita*. It is also a non-host plant for potato cyst-nematodes.

Taxonomy and diagnostic characters

Morton (1976) regarded *S. viarum* as a synonym of *S. reflexum* Schrank. However, *S. reflexum* is a synonym of *S. aculeatissimum*, a different but closely related species, see above (Nee 1991). Lester (1978) pointed out that the description given by Morton for *S. reflexum*, is that of *S. viarum*. Lester (1978) also pointed out that careful examination showed that *S. khasianum* var. *chatterjeeanum* (which is commonly, but incorrectly called simply *S. khasianum*) is *S. viarum*. More synonyms are listed by Lebrun & Stork (1997).

A good character for distinguishing *S. viarum* from all other species of section *Acanthophora* is the presence of glandular hairs on the ovary in young flowers.

In the past, specimens in South African herbaria have often been misidentified as *S. aculeatissimum*, but the combination of long straight prickles on the leaves and petioles and short curved prickles on the stems distinguishes *S. viarum* from all other members of *Solanum* in southern Africa. The density of the prickles, however, is an unreliable taxonomic character, particularly in domesticated species of *Solanum* subgenus *Leptostemonum*.

Notes

The species name probably refers to the habitat as described on the type specimen: 'Ad vias et circa domos vulgare in provinciã Brazilianã S. Pauli' (Dunal 1852).

The photograph and description published by Rhind (1969) in a popular journal for South African farmers, belong to *S. viarum* and not to the indigenous *S. panduriforme* E.Mey. ex Dunal, as claimed in the discussion accompanying the photograph.

Section *Torva* Nees in Transactions of the Linnean Society of London 17: 37–82 (1837). Type species: *S. torvum* Sw. (D'Arcy 1972).

Description: based on Whalen (1984); Jaeger (1985); Hepper & Jaeger (1986).

Large shrubs or small trees, 2–10 m high; early growth prickly on both stems and leaves; later growth usually unarmed or only sparsely prickly or bristly; sympodial units difoliate, commonly with geminate leaves; cauline pubescence of stalked or sessile stellae, varying in density, often with reduced midpoints; cauline prickles, when present, usually straight, subulate or broad-based, laterally compressed. *Leaves* petiolate, large and repand on early growth; later leaves medium to large, ovate to broadly ovate, 30–140 × 70–300 mm, entire, repand or lobed, usually unarmed, stellate-pubescent on both surfaces, with stalked stellae below, pubescence of upper surface very variable in structure and diagnostic of species. *Inflorescences* corymbose or cymose, lateral or terminal and becoming lateral by continued shoot growth, usually unarmed, remote from leaves, asymmetrically several- to many-branched, rarely simple, inflorescence branches monochasial, bearing female-sterile flowers with reduced gynoecia distally; peduncles short or well developed; pedicels unarmed, slender and flexuous in flower. *Calyx* variable, from nearly truncate to attenuate-lobed. *Corolla* white or lavender, stellate-pentagonal or less commonly deeply stelliform with narrow, nearly separate lobes. *Stamens* with anthers equal, slender and tapering. *Fruit*: berries small to medium, 5–15 mm diam., glabrous, 4-locular; pericarp tough and leathery, green, dull yellow or brown when ripe; flesh saponaceous and sticky. *Chromosome number*: $n = 12$, rarely 24, 36.

Distribution

Whalen (1984) included some 50 species in his *S. torvum* group, occurring from Mexico to southeastern Brazil, with many endemics, mostly in South America. He believed that there may also be several species indigenous to southeastern Asia and the East Indies. Two species are widely introduced in the Old World tropics. *Solanum torvum* Sw., originally from Mexico, Central America and the West Indies, is now a common introduced weed throughout the tropics of both hemispheres, but it has not been listed before for southern Africa (Welman 1993). *S. chrysotrichum* Schldl. (= *S. hispidum* auctt. non Pers.) originally from Mexico to Panama, is now widely introduced in the Palaeotropics. In the past, this species was often misidentified as *S. hispidum* Pers., but true *S. hispidum* Pers. is restricted to the Andes of southern Colombia, Ecuador and Peru.

Ecology

According to Whalen (1984), the habitat preferences of section *Torva* are variable, ranging from sea level to

over 3 000 m altitude, often in forest edges, grazed fields, and other places where direct sunlight is available. Most of the species show weedy tendencies. These large shrubs or trees are characteristic of secondary vegetation and grazed lands throughout the montane Neotropics. Species grow in understoreys and edges of montane and seasonal forest, in dry tropical woodland, in savanna, and even in subalpine elfinwoods.

Taxonomy

Bitter (1921) placed the Afro-Asian plants (series *Giganteiformia* Bitter) under the Neotropical section *Torvaria* Bitter (section *Torva* Nees). Whalen (1984) and Jaeger (1985) claimed that section *Torva* is cladistically not closely related to the Afro-Asian species, the former separating the *Giganteum* group, the latter keeping them together for convenience. Jaeger (1985) emphasized the particular differences between the neotropical *Torva* (lobate leaves, bifoliate geminate sympodial units, white flowers and firmer, larger, green to yellow fruits) and the African endemic species of the series *Giganteiformia* Bitter, raised to sectional level as *Giganteiformia* (Bitter) Child in 1998. Species of that section have plurifoliate sympodia, inflorescences with shortened, umbelloid branches, and succulent, red, translucent berries. Nee (1991) suggested that section *Acanthophora* may have been derived from the large section *Torva*.

Morphology and reproductive biology

Child (1979) noted that section *Torva* has many-flowered corymbose cymes where most flowers are hermaphrodite and fully fertile. Nee (1979) recorded that it is common in section *Torva* for the flowering branches to lack prickles, whereas the lower stem or young shoots are quite prickly. Whalen & Costich (1986) stated that section *Torva* is weakly andromonoecious, short-styled flowers are present, fruit size is small and the species are self-compatible. Child & Lester (1991) gave the following summary of section *Torva*: trifoliate sympodial units with anisophyllous geminate leaf clusters, inflorescences subsessile to pedunculate, generally lateral, leaf remote to subopposed, pleioto monochasial, pleiochasia with most flowers hermaphrodite, fully fertile, but fewer-flowered inflorescences with often only proximal flower(s) hermaphrodite, distal flowers brachystylous, functionally male, some taxa androdiocious; mostly shrubs to trees, some climbers.

Potential for crop improvement

Daunay, Lester & Laterrot (1991) noted that sterile hybrids have been obtained by artificial crosses between *S. melongena* and species of section *Torva*.

Key to naturalized species in southern Africa (after Jaeger 1985)

- 1a. Indumentum of young parts off-white; inflorescence axes with simple glandular hairs; calyx lobes in flower 4 mm long, sinuses glabrous; corolla less than 30 mm diam. *S. torvum*

- 1b. Indumentum of young parts rust-coloured; inflorescence axes and calyx sinuses not as above; calyx lobes in flower 7 mm long; corolla 30–50 mm diam. *S. chrysotrichum*

5. *Solanum chrysotrichum* Schlttdl. in Linnaea 19: 304 (1847); Shaw: 234, 238 (2000). Type: Mexico, Las Trojes, Nov., *C. Schiede 81* (HAL).

S. hispidum auctt. non Pers. (1805); D'Arcy: 703 (1973); Gentry & Standley: 121 (1974); Bailey & Bailey: 1055 (1977); Gbile: 116 (1979); Symon: 113, t. 35, 150, 161 (1981); Symon: 121 (1982); Jaeger: 346 (1985).

S. warscewiczii Hort. ex Lambertye: 429 (1865). Type: cultivated, *L. Lambertye s.n.* (W).

S. pynaertii De Wild.: 437, t. 119 (1907). Type: Boma, Congo, *L. Pynaert 302* (BR?).

Evergreen shrub or small tree up to 7 m high (in South Africa up to 3 m high), trunk up to 200 mm diam. *Prickles* 2–6 mm long, stout, usually sparse on stems, petioles and veins on upper and lower leaf surfaces, flattened towards broad, often pubescent base, straight or slightly recurved, rarely absent. *Pubescence* on all parts of stellate hairs (sessile or long, multi-seriate-stalked, porrect-stellate with medium or long central cell). *Stems* grooved and sparsely stellate when old, stem and young parts with ferruginous tomentum. *Leaves* solitary, usually broadly ovate to elliptical, ± 200–300 × ± 250–400 mm, rarely entire, margins mostly sinuate to lobed, with 7–13 lobes, sinuses cut one quarter of way to midrib, lobe apices obtuse, acute or acuminate, sinuses rounded, leaf base equal or oblique, truncate or rounded to subcordate; upper surface scabrid and covered with appressed hairs, lower surface densely covered with stellate hairs and nerves sparsely prickly; petiole up to 180 mm long, terete, with (0)3–10 prickles. *Inflorescences* extra-axillary, branched, dense scorpioid cymes with 30–50 flowers; peduncles 10–25 mm long, variable; pedicels 10–15 mm long, enlarged in fruit up to 5 mm diam. below calyx with marked corky thickening. *Calyx* densely stellate-pubescent; tube 3–4 mm long; lobes linear or lanceolate, 4–6 mm long, acuminate, in fruit broader and thicker, at first appressed, later somewhat reflexed. *Corolla* white, 30–50 mm diam., stellate; lobes 10–15 mm long, sparsely stellate-pubescent along midvein inside, densely stellate-pubescent outside, apices acute. *Stamens* with filaments 1–3 mm long; anthers 7–9 mm long, yellow, slender, erect, not coherent, tapered, dehiscing by small terminal pores and also longitudinally in basal portion of anther. *Ovary* sometimes tuberculate, ovary and style base sparsely glandular-pubescent; style 9.0–13.5 mm long, glabrous; stigma bluntly 2-lobed, pale green. *Fruit* globose, 10–15 mm diam., at first green, later yellowish to drab orange-yellow, brown when dry, glabrous, glossy, hard, not particularly fleshy, mucilaginous. *Seeds* 2–3 mm diam., flat, light brown, shiny, without obvious surface pattern, 100–250 per fruit. *Cotyledons* 4 × 10 mm, oblong; petioles 5 mm long, first true leaves ovate, scarcely lobed, not prickly until about fourth leaf. Figure 3.

Distribution

Solanum chrysotrichum is native to tropical Central America from southern Mexico to Costa Rica and Panama.

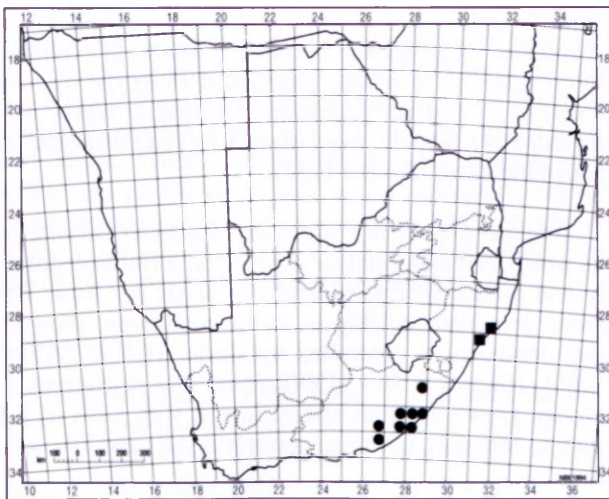


FIGURE 6.—Distribution in the FSA region, of *Solanum chrysotrichum*, ●, and *S. torvum*, ■.

It had been introduced widely in the Old World tropics as an ornamental plant, and has now been naturalized in many areas, such as in disturbed sites in the Brisbane area of Queensland (Australia) where it is known as giant devil's fig (Symon 1982). It has been collected in West Africa (e.g. Nigeria), Zimbabwe and Malawi and also in southern Africa.

In southern Africa, *S. chrysotrichum* seems to be naturalized only in Eastern Cape from about the Albany to the Libode Districts (Figure 6). The oldest record seen in this study dates from 1909, collected near Grahamstown (*Mally* A7788, GRA). It is sometimes cultivated in gardens in that province or persists as a garden relic, e.g. *Jacot Guillarmod* 4567 (GRA); *Burns, Olyott & Potts* 11 (GRA).

Ecology

In its native area, *S. chrysotrichum* is found in moist or wet thicket, sometimes in oak or oak-pine forests or in fields at 1 200–2 500 m in altitude (Gentry & Standley 1974). In South Africa it grows at an altitude of \pm 250 m, in full sun and scattered along roadsides and in other disturbed areas. It is also occasional on riverbanks and near water courses, in hillside scrub and valley vegetation where it can be found with *Zantedeschia*, *Senecio ilicifolius* and aliens like *Acacia longifolius*, *A. melanoxylon* and *Melia azedarach*. Wells *et al.* (1986) described *S. chrysotrichum* as a summer rainfall ruderal and flora weed, which does not seem to spread aggressively. In South Africa, it appears to flower almost throughout the year, while fruiting is from October to June.

Morphology

Roe (1971) described the stem hairs of *S. chrysotrichum* from Mexico as multiseriate-stalked, porrect-stellate with rather short central rays. Gbile & Sowunmi (1979) described the pollen of *S. chrysotrichum* as oblate-spheroidal with a triangular amb and indistinct sexine pattern. The polar axis is \pm 21.6 μ m and the equatorial diameter is \pm 22.0 μ m.

Chromosome number and chemistry

Fedorov (1969) reported the chromosome number $n = 12$ for *S. chrysotrichum* (as *S. hispidum*).

Dan & Dan (1984) reported that the fruits and leaves of *S. chrysotrichum* contain non-nitrogenous spirostane sapogenins and are devoid of any alkaloid. The major leaf constituents are the spirostane sapogenins neochlorogenin and paniculogenin. The chemical constituents of the roots of *S. chrysotrichum* are not known.

Uses and potential for crop improvement

No reports of any medicinal use of *S. chrysotrichum* were found in the literature. It is a garden subject in the warmer parts of the world. Khan (1979) reported that *S. chrysotrichum* had been crossed with the economically important *S. melongena* L. and produced fertile hybrids. Daunay, Lester & Laterrot (1991) reported that *S. chrysotrichum* is resistant to *Pseudomonas*, *Meloidogyne* and *Verticillium*, and partially resistant to *Thielaviopsis*, all of which attack *S. melongena*. It is also a non-host plant for potato-cyst nematodes.

Taxonomy

Most literature references to *S. hispidum* refer to *S. chrysotrichum*. True *S. hispidum* Pers. is from the Andes; the upper surface of the leaves is hairless or almost so (Shaw 2000). D'Arcy (1973) reported that *S. chrysotrichum* can hybridize with *S. torvum* in nature, at least in Panama.

Diagnostic characters and derivation of species name

Solanum chrysotrichum differs from all other species of *Solanum* in southern Africa by its coarse, reddish brown pubescence, particularly on the calyx, stems, young parts and main veins on the underside of the leaves. The species name refers to the indumentum of golden (reddish brown) hairs.

6. *Solanum torvum* Sw., *Nova genera et species plantarum*: 47 (1788); Dunal: 260 (1852); C.H.Wright: 231 (1906); Heine: 333 (1963); D'Arcy: 708 (1973); Gentry & Standley: 139, t. 19 (1974); Gbile: 118 (1979); Symon: 115, t. 36 (1981); Symon: 122 (1982); Symon: 152 (1985); Jaeger: 344 (1985); Troupin: 382 (1985); Bukenya & Hall: 86 (1988); D'Arcy & Rakotozafy: 129 (1994). Type: 'India Occidentalis' (Jamaica), O. Swartz s.n. (S, holo.).

S. mannii C.H.Wright: 129 (1894). Types: Gabon, *Sovaux* 329 (P. syn.); Fernando Po, *Mann* 55 (?K. syn.).

S. mannii C.H.Wright var. *compactum* C.H.Wright: 129 (1894). *S. torvum* Sw. var. *compactum* (C.H.Wright) C.H.Wright: 231 (1906). Types: Angola, *Welwitsch* 6105 (COL. syn.); *Welwitsch* 6052, 6080 (COL. syn.); *Monteiro* s.n. (COL. syn.).

Shrub up to 3 m high; branches terete, tomentose with yellowish brown, rarely reddish brown, stipitate-stellate and/or sessile-stellate hairs; usually armed with

few straight or recurved compressed prickles which are usually pubescent basally, up to 7×8 mm. *Leaves* \pm discolorous, solitary or sometimes in pairs, similar in shape, different in size, broadly ovate to oblong or elliptic, up to 180×250 mm, apex acuminate or acute, base mostly unequal, obtuse to subcordate, margins subentire to deeply lobed, with 2–4 pairs of lobes (uncommon in our area), upper surface scabrid with dispersed stipitate-stellate or sessile-stellate hairs, lower surface densely, softly tomentose with mostly stipitate-stellate hairs, veins rarely armed; petioles 10–100 mm long, softly stellate-hairy. *Inflorescences* lateral and internodal, corymbose cymes, several- to \pm 50-flowered, lateral, distal flowers with short styles, functionally male; inflorescence axes with simple glandular hairs; peduncles 10–30 mm long, usually 1-branched less than 100 mm from base, tomentose, hairs sessile-stellate and shortly stipitate-stellate; pedicels \pm 5 mm long, purple, drying dark, hispid-viscid with mostly glandular simple and sessile-stellate hairs, elongating up to 22 mm and thickening in fruit, then sometimes recurved. *Calyx* purplish, 3–6 mm long, hispid-viscid outside with glandular sessile-stellate hairs, glabrous within, 5-lobed; lobes 1.0–2.5 mm long initially, linear or subulate, calyx splitting with age, then lobes 2–5 mm long, lanceolate to ovate-lanceolate, apex mucronate, sinuses glabrous. *Corolla* white, 15–30 mm diam., sessile-stellate pubescent outside, glabrous within, 5-lobed; lobes lanceolate, each with prominent dark lengthwise line inside, 5–12 mm long. *Stamens* with filaments 1.0–1.5 mm long, glabrous; anthers linear-lanceolate, 6–10 mm long, often oblique basally, tapering above and dehiscing by minute terminal pores. *Ovary* globose, with short glandular, simple hairs near apex; style 8–11 mm long, curved, glabrous or sparsely glandular-hairy at base. *Fruit* globose, 10–15 mm diam., glabrous, dull, mucilaginous, produced in clusters of few to 10, yellow-green to dirty brown when ripe, drying black. *Seeds* flattened-discoid, 1.5–2.5 mm across, buff-coloured, indistinctly reticulate, \pm 350 per fruit. Figure 1.

Distribution and ecology

Solanum torvum is native to the West Indies and Meso-America, but is now a common weed throughout the humid tropics. It grows in forest areas of west, east and central tropical Africa, also in Madagascar; in southern Africa it is found in the districts of Mtunzini, Lower Tugela, Inanda and Durban in KwaZulu-Natal (Figure 6). The oldest record seen in this study dates from 1932: *Galpin 11868* (PRE) was collected on the Lower Tugela River bank, Stanger. This species was cultivated in a garden in Stellenbosch in 1937 [*Herre NBG162978* (NBG)]. In the early 1950s the Durban Botanical Station cultivated *S. torvum* from seed received from Buitenzorg, Java in 1949 [*Wager NH64099, 64100* (NH)].

In its native area, *S. torvum* is a very common weedy shrub of the lowlands and grows in dry or wet thickets, often in secondary growth, just above sea level to 1 500 m. Elsewhere it can be an aggressive weedy species in humid areas, generally at low altitudes where it becomes common in disturbed sites such as old gardens, pastures, roadsides and other waste places, also near human habi-

tation. It thrives well on good soils and grows quickly in abandoned clearings and becomes common in exploited forest reserves. It is well established along the tropical coastline of eastern Queensland (Australia) where it is regarded as a noxious weed (devil's fig) and suspected of poisoning stock (Symon 1982).

Solanum torvum is a successful colonizer because of its weedy and opportunistic characters: it fruits plentifully and produces large numbers of seeds per fruit. The seeds germinate quickly in sunlit conditions, showing that dormancy is controlled by shade (Hall & Swaine 1980). Husaini & Iwo (1990) noted that in Nigeria, *S. torvum* grows in damp places, in soil with a pH of 6.1 such as ferrasols, ferruginous tropical soils and lithosols.

In southern Africa *S. torvum* grows from about sea level to 200 m, often on red clayey sand, along river and stream banks, in swamp forest, open shrubland, coastal thorny bush and secondary scrub, often in clearings and other disturbed places. It does not seem to be an aggressive weed in this area. In KwaZulu-Natal flowering and fruiting material have been collected from April to October.

Morphology

Ahmad (1964) noted that the stomata on the lower leaf surface are 27×22 μm in size. The epidermal cell walls on the lower leaf surface are sinuous, whereas those on the upper surface are slightly sinuous. Ogunipe & Daramola (1997) found that the stomata are narrowly elliptical in surface view outline; stomata are present on both leaf surfaces. They also found that the abaxial and adaxial cells are both irregular in shape. The abaxial anticlinal cell walls are wavy while the adaxial anticlinal cell walls are wavy-sinuous. The outer periclinal walls are flat. The abaxial and adaxial cells are both $\pm 38 \times 19$ μm in size.

Ahmad (1964) noted that the hairs on both the upper and lower leaf surfaces are of two types: firstly unicellular and dagger-shaped and secondly stellate with an elongated many-celled, multi-seriate stalk bearing 4–9 rays. Bukenya & Hall (1988) found that the young leaves have dense, stalked, stellate hairs on both surfaces; mature leaves have more or less sessile, stellate hairs on the upper surface, 4–6-armed with one arm much longer than the rest, whereas the lower surface has stalked, stellate hairs of 8 or 9 more or less equal arms. Gbile & Sowunmi (1979) described the pollen of *S. torvum* as subprolate with a circular amb and distinct sexine pattern. The polar axis is ± 25.9 μm and the equatorial diameter is ± 21.2 μm .

Chromosome number and chemistry

Fedorov (1969) and Daunay, Lester & Laterrot (1991) reported a chromosome number of $n = 12$. Randell & Symon (1976) reported $n = 24$; this was confirmed by Husaini & Iwo (1990).

The roots and leaves of this species yield steroid alkaloids of the 3-aminospirostane group (Schreiber 1979).

Dan & Dan (1984) reported that the major leaf constituents of *S. torvum* are the spirostane sapogenins neochlorogenin and paniculogenin. The leaves, fruits and roots contain non-alkaloidal as well as alkaloidal sapogenins. The roots contain jurubidine which is a 3-amino-spirosolane alkaloid. Jaeger (1985) noted that the steroidal alkaloids solasodine and jurubidine as well as the sapogenins chlorogenin and neochlorogenin/paniculogenin had been recorded for *S. torvum*. Mabberley (1997) listed this species as one of the commercial sources of solasodine.

Culinary uses

Jain & Borthakur (1986) noted that in India the ripe fruits of *S. torvum* are eaten as a vegetable. Bukenya & Hall (1988) reported that the fruits are collected in some parts of Ghana and used in soup and stew. D'Arcy & Rakotozafy (1994) reported that this species is cultivated in countries like India and Myanmar for its fruits which are used as seasoning. Mabberley (1997) noted that in Sri Lanka the fruits are used in curry after the toxic seeds have been removed.

Medicinal and traditional uses

Jain & Borthakur (1986) recorded that in India *S. torvum* alone or in combination with other medicinal plants, is used for chest pain (fruits), snake bite and insect stings (leaves), stomach pain (fruits and roots), antidote to poisoning (roots), malaria (bark), night blindness (fruits), tooth infections (fruits). Lu (1986) recorded that in China the roots of this species, containing jurubidine, jurustone and other compounds, are used to 'disperse extravasated blood,' relieve pain and alleviate coughs. Gbile & Adesina (1988) noted that the ripe fruits are used for liver and spleen complaints; the fruits are expectorant and sedative. Roddick (1991) listed *S. torvum* as an antidote for various poisons, toothache, snake and insect bites and as an ingredient in malarial preparations in India and as a cough medicine and general pain killer in China.

Potential for crop improvement

Solanum torvum is graft-compatible with *S. melongena* and is resistant to *Pseudomonas*, *Meloidogyne*, *Verticillium*, *Thielaviopsis*, *Phytophthora parasitica* and the *Phytophthora* and *Fusarium solani* complex. It is resistant to *Epilachna vigintioctopunctata* and to little leaf disease, but highly susceptible to *Colletotrichum gloeosporioides*. It is a non-host plant for potato cyst-nematodes (Daunay *et al.* 1991). In Cuba *S. laciniatum* Aiton, which is cultivated as an important source of the alkaloid solasodine, has been grafted onto *S. torvum* (Esquivel & Hammer 1991).

Taxonomy

Gooding (1965) rejected the name *S. torvum* Sw. as an illegitimate and superfluous substitute by Swartz for *S. indicum* L. and replaced it with the later name *S. ficifolium* Ortega. However, Heine (1976) and Hepper (1978) pointed out that Swartz realized that Linnaeus had included both Old and New World elements under his *S. indicum* references. Swartz then grouped the West Indian element under *S. torvum*, which is a legitimate

name, with his own material as type.

Solanum torvum has become naturalized widely and as a result, numerous synonyms have been recorded (Bitter 1921; Gentry & Standley 1974; Symon 1981; Lebrun & Stork 1997). Only synonyms based on African types are listed in the present article. The fact that the leaves of this species present a great range of leaf size and lobing, depending on age and vigour, also caused several superfluous varieties to be described. In Central America it seems to hybridize with several other similar species (D'Arcy 1974); this makes the taxonomy of the section complicated.

Wright (1904) listed *S. ferrugineum* for the Durban area in KwaZulu-Natal, but described the fruit as black; Bitter (1921) believed that he was not dealing with the true *S. ferrugineum*. The specimens quoted were not seen in this study. Wright (1906) listed *S. ferrugineum* as a synonym of *S. torvum*, but Bitter (1921) disagreed with that, as he regarded these two species as related but different. D'Arcy (1973) also regarded *S. ferrugineum* as a synonym of *S. torvum*, but Nee (2001) viewed them as two distinct species.

Notes on stylar heteromorphism

Hossain (1973) studied stylar heteromorphism in *S. torvum*, the term used when two forms of flower are noticeable in each inflorescence, a character seen in several species of *Solanum*. In one form, the style is long and distinctly exerted; in the other, it is short and included within the conically connivent anthers, so that it is not visible from outside in an open flower. Hossain noted that in *S. torvum* the later-formed distal flowers have slightly reduced ovaries and much shortened styles, and so act as male flowers, forming a small proportion of the inflorescence. Only the lower flowers in any inflorescence are structurally hermaphrodite which explains the characteristic incomplete fruit set in this species.

Diagnostic characters and derivation of species name

In southern Africa *S. torvum* can be recognized by its rough, hairy leaves and its many-flowered inflorescences with fairly large white flowers and numerous large yellowish berries, drying black. Sterile specimens can be confused with *S. anguivi* Lam., but *S. torvum* has dense, fairly short-rayed stellate hairs on both sides of the leaf, whereas *S. anguivi* has fewer stellate hairs each with a single long ray or midpoint. Symon (1985) stated that since the specific epithet means savage, gloomy, grim and fierce, it could refer to the drab aspect of the plant or the stout prickles on the stems.

SPECIMENS EXAMINED

(southern Africa only)

Specimens held at PRE, unless otherwise indicated. The numbers in brackets indicate the identity of the specimens: (1) *S. aculeatissimum*; (2) *S. capsicoides*; (3) *S. mammosum*; (4) *S. viarium*; (5) *S. chrysotrichum*; (6) *S. torvum*.

Acocks 10787 (1) NH, PRE. Acocks & Hafström 1375 (1). Arnold NBG109203 (4) NBG; NBG109367 (5) NBG.

Barker 8253 (1) NBG. Bond A15 (5) GRA. Bos 1047 (1). Bottomley s.n. (3). Bradley 49 (1) GRA. Braun 1843 (4). Bredenkamp 1430 (1). Brink 276 (5) GRA, PRE; 793 (5) GRA. Burns, Olyott & Potts 11 (5) GRA.

Carbiéner PRE41371 (2). Codd 6569 (3). Connell PRE41379 (1). Cooper 1147 (1). Crawford 441 (1).

Devenish 1001, 1789 (1). De Villiers NBG10502 (1) NBG. De Winter 8251A (1). Dieterlen 887 (1) NBG, NH, PRE, SAM.

Eckhardt 465 (1) PRU.

Flanagan 1165 (1) GRA, PRE. Forbes NH34644 (1) NH. Forbes & Obermeyer 64 (2) NH, PRE. Forester 2 (1). Fourcade 992 (1) GRA. Fraser & Burns 21 (5) GRA. Froneman 8 (4) Lowveld Botanical Garden.

Galpin 11868 (6) NH, PRE; 14539 (1). Garrett 69 (4) NH. Geldenhuys 668 (1). Groenewald 146 (4) NH. Gerstner 5660 (1). Giffen s.n. (1) GRA, PRE.

Harding 39N, PRE819 (1). Henderson 737 (6); 940 (5). Herre NBG162978 (6) NBG. Hewitt A7789 (5) GRA. Hilliard 8229 (1). Hilliard & Burt 15098 (1). Hoole N6 (5) GRA; s.n. (1) GRA, PRE. Hulley s.n. (5); A7790 (5) GRA; 22 (4) NH, PRE; 40, 46, 135, 232 (4) Cedara Weeds Laboratory; 44 (1) GRA, PRE; 159 (1) Cedara Weeds Laboratory; 231 (1) GRA. Hulley & Olckers 284 (4) Cedara Weeds Laboratory, GRA; 335 (4) Cedara Weeds Laboratory. Huntley 464 (1). Hutchinson, Forbes & Verdoorn 74 (1).

Jacot Guillarmod 4567, 6836 (5) GRA; 7904 (5) GRA, PRE; Jeffery RUH4919 (1) GRA.

MacDonald 25 (5). MacOwan 1424 (1) SAM; 1493 (2) GRA. Mally A7788 (5) GRA. Marr & Harding 54 (4) NH, PRE. Martin RUH8014(c) (5) GRA. Matthews 27 (1) PRU. McCallum PRE41368 (1). McClean NH26927 (2) NH. McClean & Bayer 55 (1). McDonald & Smit 6 (1) PRU. Moffett, Daemane & Taoana 5313 (1) PRE, QWA. Mogg 1019 (1). Mohle 71 (1) Lowveld Botanical Garden, PRE. Moll 1880 (4) NH, PRE; 2191 (6) NH, PRE; 3452 (1) NH, PRE. Müller & Sheepers 223 (1).

Ngwenya 1186 (6) NH, PRE. Nicholas 2033 (1) NH. Noel RUH10623 (5) GRA.

Obermeyer 933 (1). Olckers s.n. (4) Cedara Weeds Laboratory. Oliver 7 (6) NH, PRE.

Pappe SAM18603 (1) SAM. Pegler 142 (1) GRA; 142A, 142B, 142C (1). Pentz & Acocks 10344 (6) NH, PRE. Phillipson 1198 (1) GRA, PRE. Pienaar 34 (3) NH, PRE. Pont s.n. (5). Pott TRV13649, TRV14902, TRV16808 (1). Primos SAM684203 (2) SAM.

Rogers 18078 (1). Rudatis NBG162972 (1) NBG.

Saaiman 633 (1). Sheepers 538 (1) PRE, PRU. Schlechter 6528 (1) GRA. Sim 19998 (1). Stalmans 542 (1). Stirton 6273, 6291 (1); 6306 (5); 7452 (4) NH; 8649 (4) NH, PRE.

Theron 993 (1). Thode 4218, 5134, 5135 (1) NBG. Trauseld 597 (1). Tyson 2929 (1) SAM.

Van der Schijff 4895 (1) PRE, PRU; 5636 (1). Van Vuuren 95 (1). A.E. van Wyk 13111 (1) PRU. P. van Wyk BSA2511 (6) PRU. Van Wyk & Theron 4586 (1) PRE, PRU.

Wager NH64099, NH64100 (6) NH. Ward 2884 (1) NH; 4888 (2) NH, PRE; 4897 (4); 11176 (6) NH, PRE. Watt & Breyer-Brandwijk 1205 (1). Wells 4021 (4) NH, PRE. West 1148 (1) NH, PRE. Wood 5718 (2) NH. Wylie NH22472 (1) NH.

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