

# The genus *Trichodesma* (Boraginaceae: Boraginoideae) in southern Africa

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**Keywords:** Boraginaceae, Boraginoideae, morphology, pollen, southern Africa, taxonomy, *Trichodesma* R.Br., Trichodesmeae

## ABSTRACT

*Trichodesma* R.Br. is a genus of about 45 species known from tropical and subtropical regions of Africa, Asia and Australia. The group comprises predominantly perennial herbs, the flowers characterized by anthers with prolonged connectives, often twisting above the thecae, and a prominent accrescent calyx. Five species and three subspecies of *Trichodesma* are currently recognized in southern Africa, with *T. angustifolium* Harv. subsp. **argenteum** Retief & A.E. van Wyk newly described. These taxa are widespread in southern Africa, occurring in various vegetation types. A key to the species, descriptions, distribution maps and illustrations of various micro- and macromorphological as well as palynological features are provided.

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resented by five species and three subspecies in southern Africa; about 15 species occur in Africa south of the Sahara (Lebrun & Stork 1997). Members of *Trichodesma* are widespread in southern Africa and occur in various vegetation types, ranging from grassland and savanna (bushveld) to succulent shrubland.

The purpose of this paper is to present a taxonomic revision of the genus *Trichodesma* in southern Africa. Diagnostic characters, two keys, one based mainly on fruiting characters, the other on the leaf and flowering characters, full descriptions of all species and infraspecific taxa, illustrations and distribution maps are provided. The genus and species descriptions are based on material from southern Africa and the adjacent *Flora zambesiaca* (FZ) region. This paper forms part of a revision of the Boraginaceae currently in progress for the *Flora of southern Africa* (FSA) region, henceforth referred to as southern Africa.

## INTRODUCTION

Brown described *Trichodesma* in 1810, a genus well defined by flowers with a deeply divided and strongly accrescent calyx, the absence of fornicies, anthers usually with fairly long, soft hairs on the back and conspicuous long, linear, often twisted connectives produced above the thecae. It belongs to the family Boraginaceae established by Jussieu (1789), and subfamily Boraginoideae. This family is characterized amongst others, by coiled, cymose inflorescences, setae with multicellular bases and in most genera, fruit that develop into four nutlets.

The genus *Trichodesma* R.Br. comprises ± 45 species, known from tropical and subtropical regions of Africa, Asia and Australia (Mabberley 1997). It is currently rep-

## MATERIALS AND METHODS

Herbarium specimens of *Trichodesma* in BFLU, BM, BOL, COI, E, GRA, J, K, NBG, NH, NMB, NU, PRE, PRU, SAM and WIND (acronyms as in Holmgren *et al.* 1981) were examined to gather data on morphological characters, phenology and distribution. Specimens of taxa occurring outside southern Africa that were examined, are not cited. This was supplemented by field work which included observations on the effect of fire on plants of *T. physaloides* in the Pretoria National Botanical Garden, where this species occurs naturally. Pollen and various plant parts were studied with an ISI-SX-25 scanning electron microscope. Measurements of pollen grains were done from acetolysed grains mounted in glycerine jelly. Acetolysis followed the standard method of Erdtman (1960).

## HISTORICAL OUTLINE

Brown (1810) based his concept and description of *Trichodesma* on *Borago zeylanica* Burm.f. and *B.*

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*africanum* L. When De Candolle (1846) revised the genus, he recognized eight species. In the description of *T. africanum*, De Candolle mentioned that it was collected by Thunberg and by Drège in the 'Cape of Good Hope', the first southern African record for the genus. De Candolle also included *Friedrichsthalia physaloides* Fenzl, a species previously described from the Sudan. Wright (1904) noted that *T. physaloides* (Fenzl) A.DC. also occurred in the Transvaal, South Africa. He added a third southern African species, *T. angustifolium*, described by Harvey (1859), but was not aware of *T. zeylanicum* (Burm.f.) R.Br., today also known from southern Africa, although originally described from Sri Lanka (Ceylon), and most probably introduced to the region by man. Two species, *T. africanum* and *T. angustifolium*, were recognized in the flora of South West Africa (now Namibia) by Friedrich-Holzhammer (1967). Herman (1993) listed five species and a subspecies for southern Africa, namely *T. africanum*, *T. angustifolium*, *T. arenicola* Gürke, *T. physaloides*, *T. zeylanicum* and *T. ambacense* Welw. subsp. *hockii* (De Wild.) Brummitt. However, specimens from southern Africa previously identified as *T. arenicola*, proved to be *T. ambacense* Welw. subsp. *hockii*. In the present paper we recognize five species and three subspecies of *Trichodesma* in southern Africa, namely *T. africanum* (L.) Lehm., *T. ambacense* Welw. subsp. *hockii* (De Wild.) Brummitt, *T. angustifolium* Harv. subsp. *angustifolium*, *T. angustifolium* Harv. subsp. *argenteum* Retief & A.E. van Wyk subsp. nov., *T. physaloides* (Fenzl) A.DC. and *T. zeylanicum* (Burm.f.) R.Br. Brummitt (1990), in his account on *Trichodesma* for the *Flora zambesiaca* (FZ) region, recognized the same species for the FZ region except for *T. africanum*, a species with a disjunct distribution between the FSA region, Angola and North Africa, and which is not known in the region. *T. zeylanicum*, *T. physaloides* and *T. ambacense* extend further north into Africa, supplemented by other species (Verdcourt 1991).

#### TRIBAL DELIMITATION

De Candolle (1846) assigned *Trichodesma* to the tribe 'Borragaeae' and subtribe Cynoglosseae, a classification followed by most subsequent authors, for example Hooker (1885), Gürke (1897), Baker & Wright (1905), Brand (1921), Melchior (1964) and Hilger (1985). In 1941 Zakirov placed *Trichodesma* in a tribe of its own, Trichodesmeae, recognized by Riedl (1967) and is also accepted in the present contribution. *Trichodesma* is well defined by a combination of floral and palynological characters: deeply divided and strongly accrescent calyx; the absence of fornicies in the corolla tube; anthers that usually have fairly long, soft hairs on the back; and conspicuous long, linear, often twisted connectives above the thecae. Pollen of the genus shows essentially no interspecific differences, is isopolar, tricolporate and with a nodular tectum. This pollen type is strikingly different from that of most genera of the tribe Cynoglosseae in which the grains are heterocolpate and the tectum psilate (Retief & Van Wyk 1999a, b). Avetisian (1956) agreed with Zakirov in removing *Trichodesma* from the tribe Cynoglosseae, based on the structure of its flowers and fruits, because the pollen grains of the genus have nothing in common with those of the Cynoglosseae.

Pollen morphology thus strongly supports the recognition of the separate tribe, Trichodesmeae.

Members of *Trichodesma* differ significantly from each other in nutlet morphology (see note on fruit morphology). However, the presence of glochidia on the outer surface of the nutlets of *T. africanum* and *T. angustifolium* could be used to argue that the placement of *Trichodesma* in its own tribe is not justified, because glochidia also occur on the outer nutlet surface of *Cynoglossum* and *Afrotysonia*. The types of glochidia found in *Trichodesma*, however, differ from those of *Cynoglossum* and *Afrotysonia*. Hilger (1985) studied the development and morphology of flowers and fruits of 23 species of the Cynoglosseae and Eritrichieae, and commented on the implications of his findings on the taxonomy of these groups. He found that in most Cynoglosseae the nutlets are initially positioned with their disc (the flat base) parallel to the basal area (the nectary disc) of the gynoeceum. Subsequent growth in a vertical direction brings the nutlets to their final oblique position. In both species of *Trichodesma* studied by Hilger, he observed that the nutlets are, from the beginning, in an oblique position. This can also be used to support the recognition of a separate tribe for this genus.

Two other genera are assigned to the tribe Trichodesmeae, namely *Caccinia* Savi and *Suchtelenia* Kar. ex Meisn. (Riedl 1967). Gürke (1897) separated five genera using the accrescent calyx, either enclosing the fruit or expanded, as the key character: *Trichodesma*, *Suchtelenia*, *Caccinia*, *Brachybotrys* Maxim. ex Oliv. and *Heliocarya* Bunge. *Heliocarya* is regarded as congeneric with *Caccinia* (Mabberley 1997) and *Brachybotrys* belongs to the tribe Trigonotideae (Riedl 1997). *Suchtelenia* has 6-heterocolpate pollen grains, showing similarity to pollen of members of Heliotropioideae, Cynoglosseae, Eritrichieae and Myosotioideae. The triaperturate pollen grains of *Trichodesma* and *Caccinia*, on the other hand, show similarity to pollen of the subfamilies Wellstedioideae and Ehretioideae. The tribe Trichodesmeae can be regarded as 'primitive' within the subfamily Boraginoideae, showing similarities to various other genera within the Boraginaceae *s.l.* The family is sometimes treated as two separate entities, Boraginaceae *s. str.* and Ehretiaceae, but various characteristics support the recognition of one family divided into several subfamilies (Retief & Van Wyk 1999c).

#### MORPHOLOGICAL CHARACTERS OF TAXONOMIC SIGNIFICANCE

##### *Habit*

*Trichodesma* is a genus of perennial and annual herbs or subshrubs. *T. africanum* is the only southern African species that is usually annual or occasionally biennial. This growth form can be correlated with its distribution in arid and desert regions where fast growth under optimal conditions is essential.

The other species are perennial herbs or subshrubs occurring in summer rainfall regions, mainly in grassland and savanna. They are subjected to winter drought and

also to regular natural fires and frost. Grassland species are usually quick in responding to the effects of fire (smoke, change in temperature and the release of nutrients), and plants may sprout a number of inflorescences. With sturdy, often very old, fire-resistant rootstocks and mass seed production by fire-stimulated flowering, these species are well-adapted to survive unfavourable conditions. Most examples of fire-stimulated flowering plants do flower in the absence of fire, but not as profusely as when subjected to fire. It was, however, observed that unburned plants of *T. physaloides* did not flower at all or produced only a few inflorescences, as opposed to burned plants of the species in the same grassland that sprouted and produced inflorescences abundantly after a natural fire (Figure 1A, B). Burning of this particular piece of grassland under controlled circumstances to remove moribund and/or unacceptable grass material had no effect on the number of flowers produced, because the intensity of the fire was too low. A cool or low-intensity fire of less than 1 000 kJ/s/m is usually applied (Trollope 1992).

### Leaf

Intraspecific taxa of *Trichodesma* differ remarkably in the indumentum of the leaf blade. The leaf trichome complement of the southern African members of *Trichodesma* consists of setae with multicellular bases, and simple, unbranched hairs. *T. physaloides* and *T. ambacense* subsp. *hockii* have flat, large-based setae, but differ in the structure of the setae (Figure 2A, B, D, E). *T. ambacense* subsp. *hockii* (Figure 2D) has slender setae, orientated in different directions, whereas *T. physaloides* (Figure 2E) has shorter, attenuate setae, orientated more or less in a direction parallel to the midrib. Upper leaf surfaces of the taxa concerned are relatively densely hairy (Figure 2A, C, H), whereas the lower leaf surfaces of *T. physaloides* (Figure 2B), *T. ambacense* subsp. *hockii*, *T. angustifolium* subsp. *angustifolium* and *T. africanum* (Figure 2I) are sparsely hairy, with setae scattered on the midribs and along the veins. *T. angustifolium* subsp. *angustifolium* is characterized by an indumentum of appressed setae, orientated in a direction parallel to the midrib and varying in length and in size at the base, with distinct spaces between the trichomes. The

leaf surfaces of *T. angustifolium* subsp. *argenteum* (Figure 2C, F) are silver-grey, covered with a dense layer of setae on both surfaces, a feature distinguishing this taxon from all other southern African taxa of *Trichodesma*. The outline of the multicellular bases of the setae is not circular, but slightly asymmetrical.

Leaves of *T. zeylanicum* (Figure 2G) are characterized by a lower surface that is densely hairy, with mainly simple, small hairs, but also with scattered setae along the midrib and some veins. The upper surface is covered by setae of which the large, 2-layered multicellular bases are  $\pm$  circular in outline, with much smaller setae in between (Figure 2H). *T. africanum* has a spinose indumentum with stiff setae on the lower surface (Figure 2I). Cells of the multicellular base of the setae are narrower compared to those of *T. zeylanicum*. The upper surface of *T. africanum* is characterized by well-spaced setae with a prominent row of swollen cells at the point where the seta and multicellular base join. Cells of the multicellular bases of the older leaves are impregnated with silica and some calcium, giving them a spotted appearance.

### Flower

Various flower characters in *Trichodesma* are taxonomically significant. Anthers with connectives lengthening into usually twisted appendages above the thecae, distinguish the genus from all other southern African members of the family (Figure 3A, B). Long, shaggy hairs (Figure 3A, C, F) are present on the dorsal surfaces of the connectives, whereas the inside of the thecae are glabrous (Figure 3F). The subglobose stigma displays two types of receptive surfaces (Figure 3D, E, G, H). *T. angustifolium* has papillae with prominent contiguous caps (distal swellings) and crenulate margins (Figure 3D, E). Papillae without distinct caps occur in the other taxa studied (Figure 3G, H). Corolla lobes are often twisted (Figure 3I) and acuminate to long-acuminate. The colour of the lobes is usually shades of blue except for *T. physaloides* which has white lobes with a brownish rim.

A prominent feature of the flower in *Trichodesma* is the calyx which is strongly accrescent when in fruit



FIGURE 1.—*Trichodesma physaloides*. A, plant in unburned grassland; B, plant flowering abundantly after a natural veld fire.

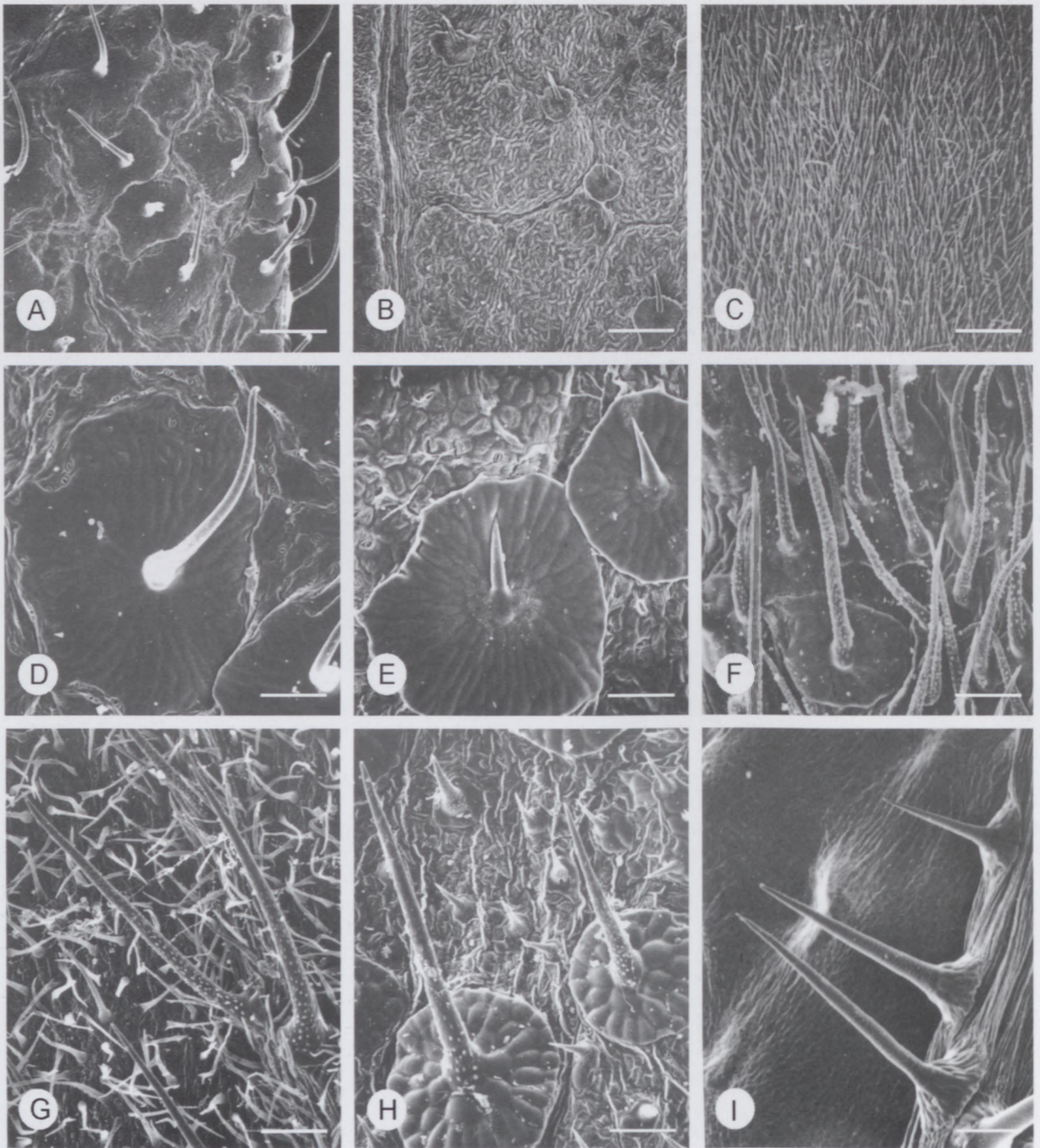


FIGURE 2.—*Trichodesma* leaf surfaces. A, *Trichodesma ambacense* subsp. *hockii*, Schoenfelder 159, upper surface; B, *T. physaloides*, Jacobsen 1813, lower surface; C, *T. angustifolium* subsp. *argenteum*, Retief 1404.01, upper surface; D, *T. ambacense* subsp. *hockii*, Schoenfelder 159, setae, slightly hooked, on upper surface; E, *T. physaloides*, Onderstall 1248, stiff setae on upper surface; F, *T. angustifolium* subsp. *argenteum*, Retief 1404.01, slender setae on upper surface. G, H, *T. zeylanicum*, Stalmans 1076: G, lower surface; H, upper surface. I, *T. africanum*, Smook 7695, stiff setae on midrib of lower surface. Scale bars: A, G 18  $\mu$ m; B, 11  $\mu$ m; C, 8  $\mu$ m; D, 49  $\mu$ m; E, 26  $\mu$ m; F, 51  $\mu$ m; H, 2  $\mu$ m; I, 37  $\mu$ m.

(Figure 4). *T. physaloides* and *T. ambacense* subsp. *hockii* are characterized by a single mature nutlet with a persistent style. The style is initially gynobasic, but due to abortion of three ovules, it becomes orientated sideways. These single nutlets, together with the calyx and style are shed from the plant. This type of nutlet dispersal also occurs in *Cryptantha flava* (A.Nels.) Payson, another member of the Boraginaceae. According to Casper & Wiens (1981), the abortion of three of the four ovules may be an adaptation for dispersal by wind, the entire floral structure serving as a relatively light disper-

sal unit. The attached, accrescent, papery calyx may augment the buoyancy of nutlets in air currents and increase the dispersal distance. In the case of *T. africanum* it can be speculated that the spinose indumentum of the calyx protects the nutlets, allowing them to mature before any damage can be done by herbivores.

#### Pollen

Pollen studies revealed no significant differences between the species of *Trichodesma* included in this

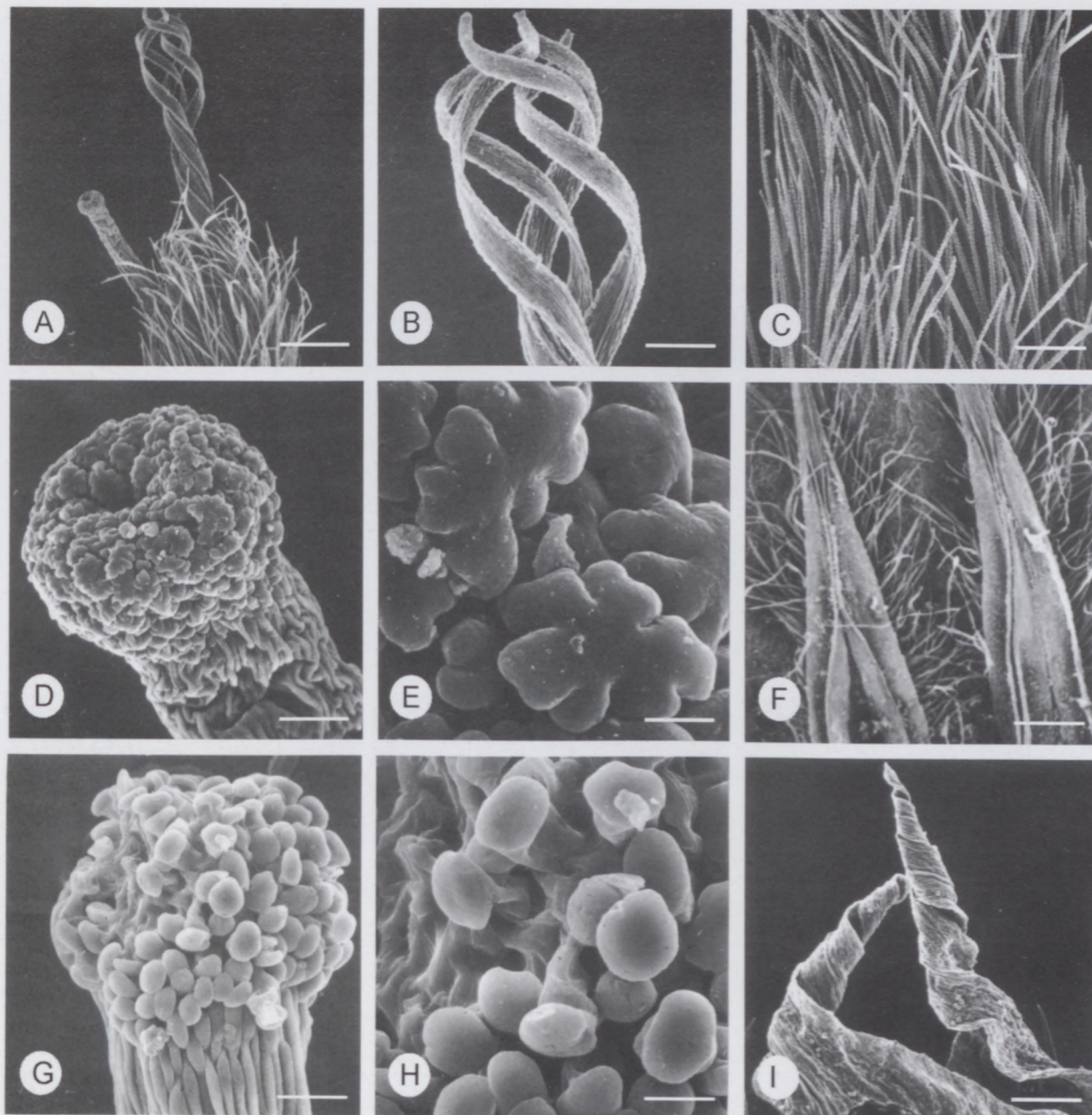


FIGURE 3.—*Trichodesma* flower parts. A–E, *Trichodesma angustifolium* subsp. *angustifolium*, Peeters, Gericke & Burelli 163: A, style, stigma and upper parts of anthers; B, twisted connectives; C, hairs on back of anthers; D, stigma; E, papillae. F, *T. physaloides*, Fourie 2804, section of two anthers. G–I, *T. africanum*, Germishuizen 4575: G, stigma; H, papillae; I, twisted apices of corolla lobes. Scale bars: A, 375  $\mu$ m; B, 178  $\mu$ m; C, 264  $\mu$ m; D, 51  $\mu$ m; E, 8  $\mu$ m; F, 750  $\mu$ m; G, 40  $\mu$ m; H, 18  $\mu$ m; I, 259  $\mu$ m.

study, a finding that is in agreement with Brummitt (1982). Pollen grains of the genus are isopolar, radially symmetrical, tricolporate, subspheroidal, with  $P = 7.0\text{--}11.5 \mu\text{m}$ ,  $E = 6.0\text{--}9.5 \mu\text{m}$ ,  $P/E = 1.1\text{--}1.2$  (Figure 5A–F). The shape of the pollen grains in polar view is  $\pm$  triangular, with convex mesocolpia and sunken apertures (Figure 5B). The equatorial view is elliptic to rounded with protruding ora; grains are angulaperturate (Figure 5A, C). Long apertures, extending over about  $4/5$  of the length of the polar axis, are characteristic of the grains. They are comparatively narrow with acute ends and the margins are not conspicuously different. Ora are coarsely granular, with endo-apertures alongate (Figure 5D). The tectum is nodular with nodules  $\pm$  of the same size (Figure 5E), sometimes absent in the vicinity of the ora (Figure 5C, D). As noted in the discussion on the tribal delimitation of the genus, some authors prefer to classify

*Trichodesma* in the tribe Cynoglosseae but the tricolporate pollen of the genus supports its placement in the separate tribe Trichodesmeae. Pollen grains of members of the tribe Cynoglosseae are usually heterocolpate, quite different from those of *Trichodesma*. The similarity in pollen morphology between *Trichodesma* and *Cordia*, does not support the separation of the Boraginaceae into two separate families (Retief & Van Wyk 1999a).

#### Fruit

In Boraginaceae fruit characters are often used to distinguish species. Brand (1921) recognized six sections in *Trichodesma*, based on the outer surface morphology of the nutlets. Members of four sections are present in southern Africa, similar to the diversity reported by Verdcourt (1991) for East Africa. *T. physaloides* and *T.*



FIGURE 4.—*Trichodesma physaloides*. Mature fruit and accrescent calyx,  $\times 1$ . Retief 2223 (PRE).

*ambacense* subsp. *hockii* (sect. *Friedrichsthalia* (Fenzl) A.DC.) are characterized by a single,  $\pm$  circular, cushion-

shaped, silken-haired nutlet (Figures 4; 6A; 10E). Nutlets of *T. physaloides* are covered with thin attenuate hairs (Figure 6B), whereas those of *T. ambacense* var. *hockii* have an indumentum of hooked hairs (Figure 6C). The other species have a fruit of four nutlets and are divided into two groups. Nutlets of *T. zeylanicum* (sect. *Trichodesma*) are emarginate and smooth on the outer face (Figure 6F), but rugose on the inner face. *T. angustifolium* (sect. *Acanthocaryum* Brand) and *T. africanum* (sect. *Serraticaryum* Verdc.) are characterized by the presence of glochidia (Figure 6D, E, G). The glochidia differ, however, in structure (Figure 6E, G). *T. angustifolium* is characterized by much smaller barbs than *T. africanum*. Nutlets of *T. africanum* are ovoid-cup-shaped with distinct, serrate, raised margins and a concave, glochidiate inner face (Figure 6G, H). The family Boraginaceae is characterized by flat, conical or pyramidal gynobases as e.g. in *T. africanum* where the gynobase is pyramidal (Figure 6I).

#### PHYTOGEOGRAPHY

*Trichodesma* is widespread in southern Africa (Figure 7) where members occur in various vegetation types,

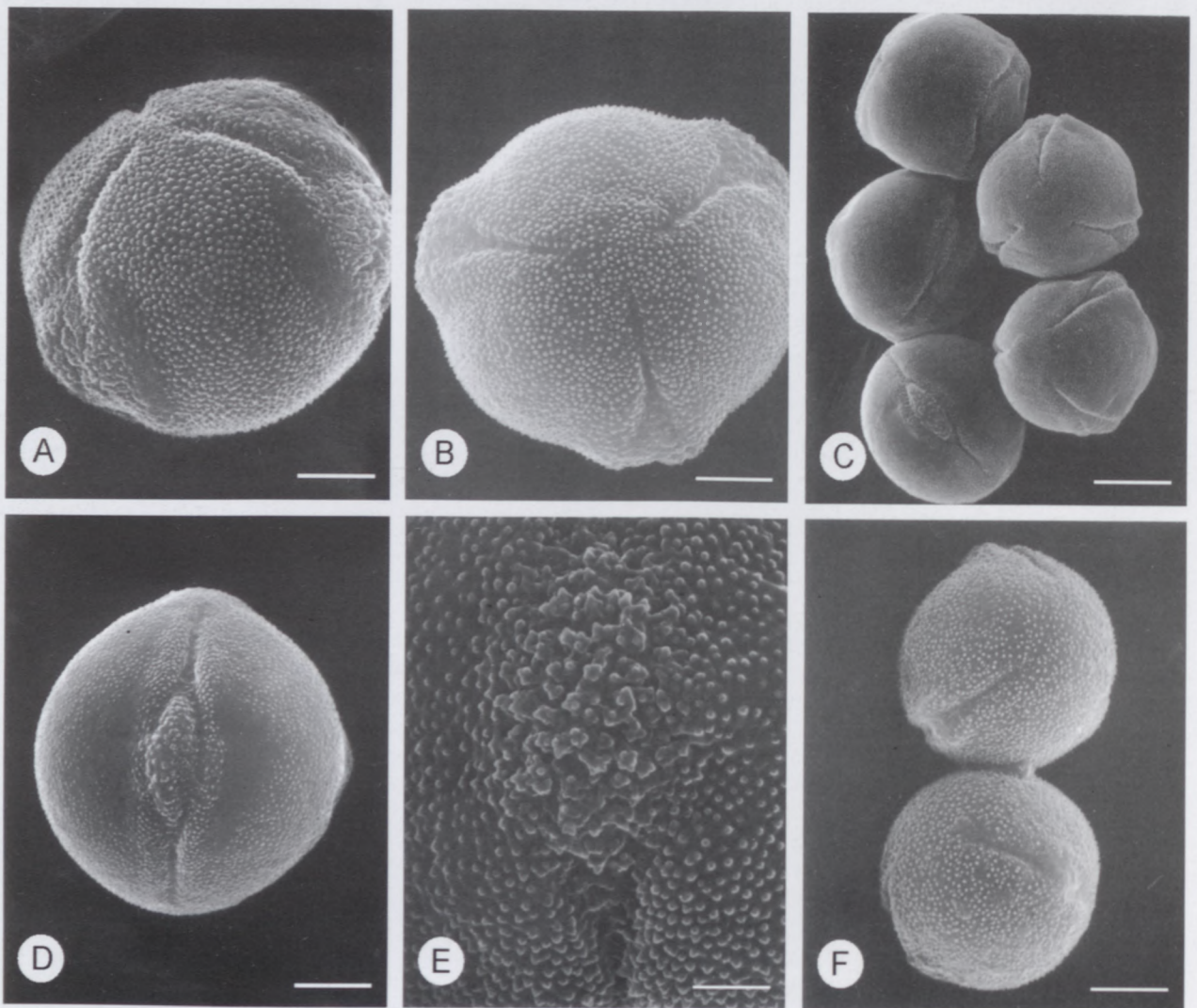


FIGURE 5.—*Trichodesma* pollen. A–E: unacetolysed; F, acetolysed. A, B, *T. africanum*: A, Germishuizen 4575, side view; B, Nicholas 2576, polar view. C, D, *T. zeylanicum*, Strey 5656: C, group; D, equatorial view of grain. E, *T. angustifolium* subsp. *angustifolium*, Hanekom 1498, tectum; F, *T. ambacense* subsp. *hockii*, Codd 7416, group. Scale bars: A, B, 2.8  $\mu\text{m}$ ; C, 6.5  $\mu\text{m}$ ; D, 3.2  $\mu\text{m}$ ; E, 1.0  $\mu\text{m}$ ; F, 4.8  $\mu\text{m}$ .

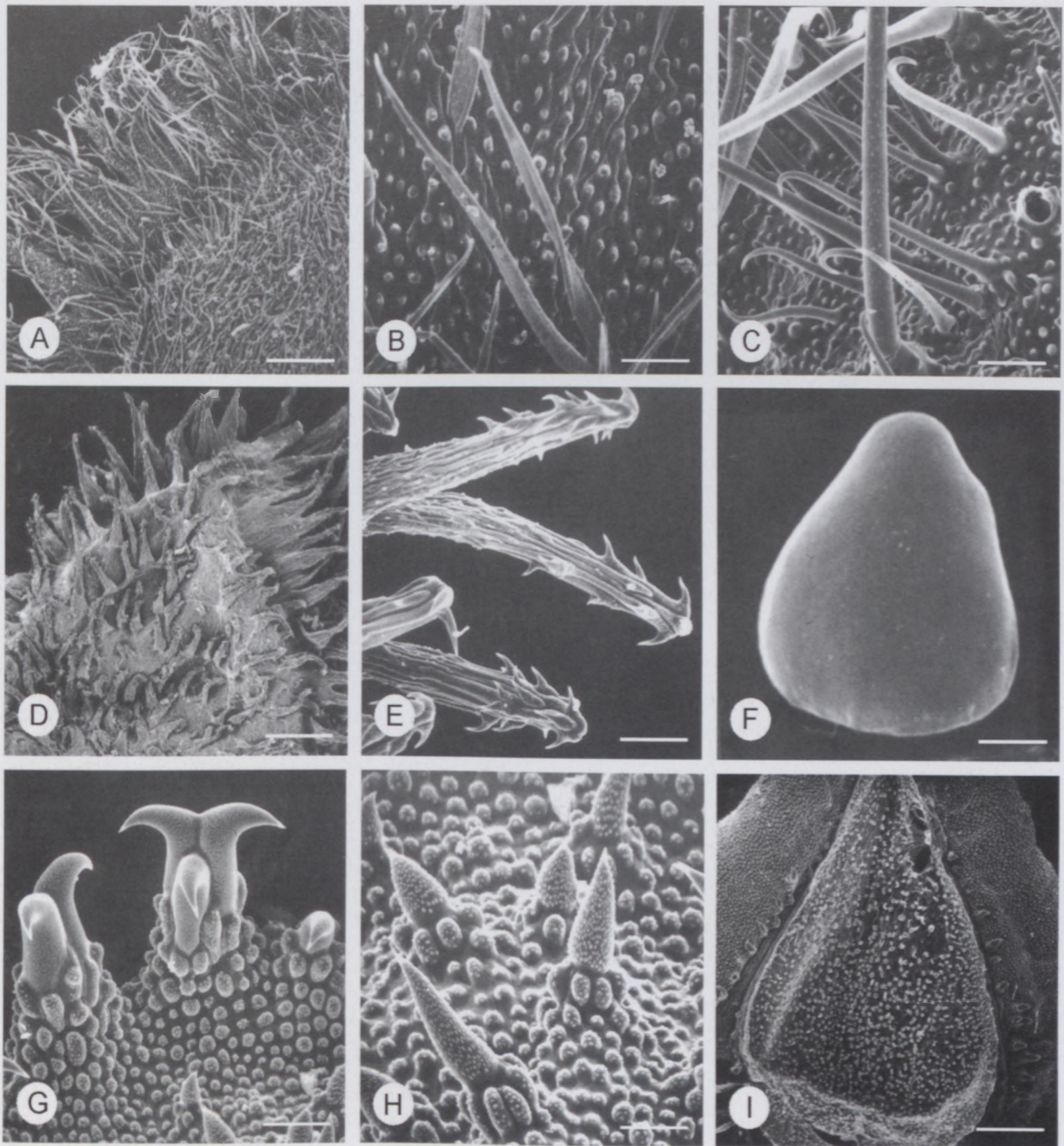


FIGURE 6.—*Trichodesma* nutlet surfaces. A, *T. physaloides*, JBG6150, margin; B, hairs; C, *T. ambacense* subsp. *hockii*, Schoenfelder 159, hooked hairs. D, E, *T. angustifolium* subsp. *angustifolium*: D, Gerstner 5133, glochidiate surface; E, Hanekom 1498, glochidia. F, *T. zeylanicum*, Netshungani 915, smooth nutlet. G–I, *T. africanum*: G, Bengis 463, margin with glochidia; H, Bengis 463, setae on dorsal surface; I, Van Jaarsveld 8825, pyramidal gynobase, one nutlet removed. Scale bars: A, 838  $\mu$ m; B, C, 84  $\mu$ m; D, 749  $\mu$ m; E, 131  $\mu$ m; F, 713  $\mu$ m; G, 79  $\mu$ m; H, 49  $\mu$ m; I, 419  $\mu$ m.

ranging from grassland and savanna to succulent shrubland, mainly in the Savanna and Grassland Biomes. All southern African species extend further north into Africa.

*Trichodesma angustifolium* subsp. *argenteum*, occurring in the northern parts of Namibia, is the only taxon endemic to the FSA region. Brummitt (1985) described a new *Trichodesma* species from the volcanic regions of Kenya, *T. marsabiticum* Brummitt, which is very similar in facies to *T. angustifolium*, and can be regarded as a vicariant of the southern African species, which differs in calyx and corolla characters. *T. angustifolium* subsp. *angustifolium* itself is disjunct in distribution in southern

Africa (Figure 9), and its current occurrences may represent relicts of a once much wider distribution. Brummitt (1985) considered that an early record of the species from Bulawayo in Zimbabwe should be disregarded unless modern collections can substantiate it.

The floristic connection between the dry areas of southern Africa, especially Namibia, and northeastern tropical Africa is well known, and is ascribed to a so-called arid corridor which connected the two regions at various times in the past (Verdcourt 1969; De Winter 1971; Thulin & Johansson 1996). *T. africanum* and *T. angustifolium* are examples of species confined to arid

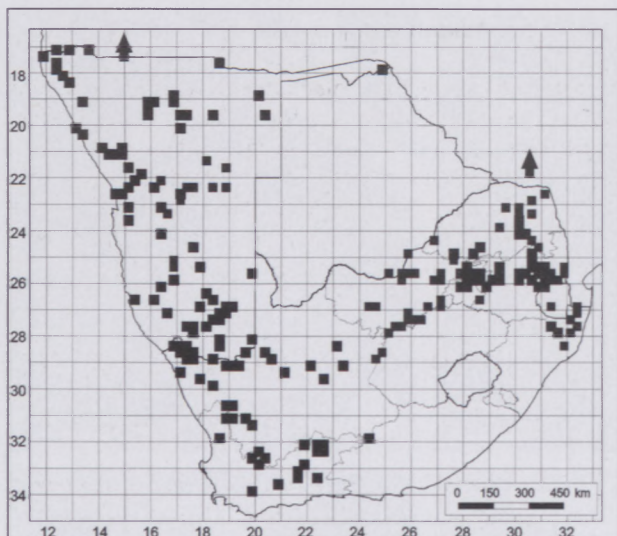


FIGURE 7.—Distribution of *Trichodesma* in southern Africa.

climatic conditions: in Africa it is known from arid parts of southern Africa, Angola and North Africa, thus belonging to the disjunct Afro-arid element.

The genus *Trichodesma* occurs in all six phytogeographical regions of southern Africa recognized by White (1983): Zambesian region, Kalahari-Highveld Transition Zone, Karoo-Namib Region, Tongaland-Pondoland Region, Afromontane Region and Cape Region. *T. physaloides* occurs mainly in the Afromontane floristic region which extends from the northern parts of Africa to southern Africa along the eastern mountain ranges. The Afromontane region comprises a series of isolated highland areas and is well represented in eastern Africa from Yemen to South Africa, but is also present in the Cameroon (Denys 1980). The region in southern Africa is characterized by numerous small forest patches in a grassland or fynbos matrix. The edges, or ecotones between forests and grasslands are usually sharp (typically just over a few metres) and are mainly maintained by both natural and more anthropogenic fires. *T. ambacense* subsp. *hockii*, closely related to *T. physaloides*, is found in some regions where *T. physaloides* occurs but is also found in regions such as Nigeria (see Brummitt 1985).

*Trichodesma zeylanicum* is an ancient Old World weed of human cultivation, introduced in southern Africa, ± 1905. It is no longer possible to distinguish natural occurrences of this species from introductions, hence its original native region is uncertain. *T. zeylanicum* occurs in grassland, woodland, in dry river beds, is a common weed in old and new cultivated land, a pioneer in disturbed areas, and is found along roadsides. The species is known from Namibia (Caprivi), the eastern parts of Northern Province, Mpumalanga, Swaziland and northern KwaZulu-Natal.

#### TAXONOMIC TREATMENT

*Trichodesma* R.Br., Prodr. fl. novae Hollandiae: 496 (1810), nom. conserv.; Harv.: 241 (1838); A.DC.: 172 (1846); Benth.: 845 (1876); Hook.f.: 153

(1885); Gürke: 99 (1897); C.H. Wright: 10 (1904); Baker & C.H. Wright: 44 (1905); Brand: 19 (1921); E. Phillips: 628 (1951); Friedr.-Holzh.: 2 (1967); Riedl: 219 (1967); Kazmi: 515 (1971); Taton: 36 (1971); Kabuye & Agnew: 520 (1974); S.P. Banerjee & Pramanik: 109 (1975); R.A. Dyer: 510 (1975); J.R. Edm.: 435 (1978); Qaiser: 31 (1979); Tölken: 1172 (1986); Brummitt: 94 (1990); Nowicke & J.S. Mill.: 24 (1991); Verdc.: 91 (1991); E.S. Martins & Brummitt: 61 (1993); Riedl: 124 (1997); Retief: 182 (2000). Type: *Trichodesma zeylanicum* (Burm.f.) R.Br. (= *Borago zeylanica* Burm.f.)

*Borraginoides* Boehm.: 18 (1760). *Pollichia* Medik.: 247 (1783); non *Pollichia* Aiton: 5 (1789). *Boraginella* Kuntze: 435 (1891). Type: *Borago indica* L.

*Friedrichsthalia* Fenzl: 53 (1839). Type: *Friedrichsthalia physaloides* Fenzl.

*Leiocarya* Hochst.: 30 (1844). Type: *Leiocarya kotschyana* Hochst.

Annual and perennial herbs, often with annual stems from a woody rootstock, variously hairy. *Leaves* simple, opposite, subopposite or alternate, basal leaves usually opposite and petiolate, upper ones alternate and sessile or all leaves sessile, diminishing in size towards inflorescences; blade variously shaped, entire; stipules absent. *Inflorescence* a scorpioid, cymose panicle, bracteate, usually terminal. *Flowers* bisexual, regular, pedicellate, calyx, corolla and stamens usually 5-merous. *Calyx* deeply divided to base or lobes loosely adherent along lower margin, finely setulose on abaxial side, variously hairy on adaxial side; lobes ovate or narrowly ovate, sometimes winged, base rounded to cordate, apex acute, acuminate or cuspidate, strongly accrescent and papery in fruit. *Corolla* blue or white; tube campanulate or funnel-shaped, naked in throat, but with gibbosities between lobe sinuses; lobes ovate to broadly triangular, apex truncate or acute to acuminate, sometimes cuspidate, often spreading or reflexed. *Stamens* arising from base or from throat of corolla tube, sessile or filaments shorter than 1 mm and broader than long; anthers linear-oblong or linear-lanceolate, with long hairs on back, connectives prolonged above anthers, often twisted together at apex, usually exerted. *Ovary* 4-lobed, with a single ovule in each loculus; style persistent, gynobasic, terete, narrowing above; stigma subglobose, papillate, papillae with or without distinct caps, caps with crenulate margins. *Fruit* either 4 nutlets or by abortion 1; nutlets ovoid, planoconvex or biconvex, smooth or variously ornamented.

The name *Trichodesma* alludes to the twisted hairs or awns that terminate the anthers; Greek *thrix*, *trikhos* = hair and *desme* = a band or bundle (Tölken 1986).

Brand (1921) divided the genus into six sections but his taxonomy and nomenclature have been queried since. Some of the rather striking differences could be considered almost of generic importance (Verdcourt 1991), but we found no supporting palynological differences to justify this view in agreement with Brummitt (1982). Five species and three subspecies are recognized in southern Africa. Southern African species of *Trichodesma* represent the following four sections:



Sect. **Trichodesma**; Riedl: 225 (1967).

Fruit of four emarginate, smooth, shining nutlets, gynobase pyramidal with four strongly concave sides, each with  $\pm$  winged margin; nutlets compressed-ovoid, outer face usually mottled with grey and brown, inner face rugose, covered with indistinct papillae (*T. zeylanicum*).

Sect. **Serraticaryum** Verdc.: 92 (1991) (sect. *Friedrichsthalia* Brand non (Fenzl) A.DC.).

Fruit of four nutlets, ovoid-cup-shaped with distinct serrate margins and glochidiate hairs on outer face, i.e. base of cup; outer face convex, inner face concave, serrate margin also with glochidia; gynobase pyramidal with four strongly concave sides, each with  $\pm$  winged margin, verrucose (*T. africanum*).

Sect. **Acanthocaryum** Brand: 27 (1921).

Fruit of four nutlets, glochidiate, marginal glochidia usually coalescing at bases to form distinct rim; gynobase pyramidal with four strong concave sides, each with  $\pm$  winged margin; nutlets compressed-ovoid (*T. angustifolium*). Brummitt (1992) suggested that this section might be combined with sect. *Friedrichsthalia* Brand non (Fenzl) A.DC., now sect. *Serraticaryum* Verdc.

Sect. **Friedrichsthalia** (Fenzl) A.DC.: 173 (1846).

Fruit a single,  $\pm$  circular, cushion-shaped, silken-haired nutlet, concealed in accrescent calyx until released, attached by most of its lower surface to receptacle; gynobase flat; style persistent, lateral (*T. ambacense* subsp. *hockii*, *T. physaloides*).

Key to species  
(based on fruiting characters)

- 1a Fruit of four nutlets:  
 2a Nutlet with outer surface smooth and shiny; lower leaf blade surface with setae only along midrib and veins, intercostal surfaces with dense cover of small bulbous-based hairs, orientated in different directions. upper leaf blade surface covered with long and much smaller setae in between ..... 1. *T. zeylanicum*  
 2b Nutlet with outer surface glochidiate; indumentum of leaf blade not as above:  
 3a Glochidia thick, mainly along serrate, raised margin of nutlet, thick short setae on dorsal side of nutlet; leaf blade ovate to narrowly ovate, lower surface with tubercle-based, stiff setae usually only along midrib and veins, upper surface with well-spaced, discoid-based setae ..... 2. *T. africanum*  
 3b Glochidia slender, covering whole surface of nutlet; leaf blade linear to narrowly elliptic, lower and upper surfaces with well- to densely spaced, discoid-based, slender setae ..... 3. *T. angustifolium*  
 1b Fruit a single nutlet:  
 4a Corolla lobes white with a light brown rim, rounded to truncate with short cuspidate apices; lower leaf blade surface with short, stiff, discoid-based setae scattered on midrib and veins, upper leaf blade covered with similar setae well spaced ..... 4. *T. physaloides*  
 4b Corolla lobes blue or rarely whitish,  $\pm$  triangular, with long acute apices; lower and upper leaf blade surfaces with broad, discoid-based, slender setae, well spaced ..... 5. *T. ambacense*

Key to species  
(based on leaf and flower characters)

- 1a Leaf blade linear to narrowly elliptic ..... 3. *T. angustifolium*  
 1b Leaf blade broadly ovate, ovate, narrowly ovate or elliptic:  
 2a Corolla lobes scarcely spreading when fully developed, rounded to truncate, cuspidate white and with a brownish rim; leaf blade sparsely hairy with stiff, short setae ..... 4. *T. physaloides*  
 2b Corolla lobes reflexed over calyx when fully developed, acute to acuminate at apices, blue or rarely whitish, not with a brownish rim; leaf blade hairy, setae slender:  
 3a Accrescent calyx lobes cordate at base,  $\pm$  22  $\times$  15 mm in fruit ..... 5. *T. ambacense*  
 3b Accrescent calyx lobes  $\pm$  rounded at base:  
 4a Stems, inflorescence axes and calyx spinously hairy; lower leaf surfaces sparsely hairy with setae scattered along midribs and veins ..... 2. *T. africanum*  
 4b Stems, inflorescence axes and calyx patently hairy; lower leaf surfaces with setae only along midribs and veins, intercostal surfaces with a dense cover of small, bulbous-based hairs, orientated in different directions ..... 1. *T. zeylanicum*

1. ***Trichodesma zeylanicum*** (Burm.f.) R.Br., *Prodromus florae novae hollandiae*: 496 (1810); A.DC.: 172 (1846); A.Rich.: 91 (1850); Hook.: t. 4820 (1854); Klotzsch: 255 (1861); Gürke: 99 (1897); Baker & C.H.Wright: 51 (1905); Brand: 40 (1921); F.W.Andrews: 90 (1956); Ivens: 83

(1967); Taton: 37 (1971); Kabuye & Agnew: 520 (1974); S.P.Banerjee & Pramanik: 109 (1975); Tölken: 1172 (1986); Brummitt: 95 (1990); Nowicke & J.S.Mill.: 25 (1991); Verdc.: 92 (1991); E.S.Martins & Brummitt: 62 (1993); Retief & P.P.J.Herman: 354 (1997); Riedl: 125 (1997). Type: Ceylon, *Garcin* in *Herb. Burm.* (G, lecto.-K, photo.!).

*Borago zeylanica* Burm.f.: 41 (1768). *Pollichia zeylanica* (Burm.f.) F.Muell.: 100 (1882). *Boraginella zeylanica* (Burm.f.) Kuntze: 435 (1891). *Boraginoides zeylanica* (Burm.f.) Hiem: 720 (1898).

*Leiocarya kotschyana* Hochst.: 30 (1844). Types: Ethiopia, Djelajeranne, *Schimper* 625 (B, syn.†, BM, K! isosyn.) & Sudan, Nubia, Camamil and Gebbel Kassan, *Kotschy* 542 (B†, K!, W, isosyn.).

Erect, perennial herb with annual stems from a woody rootstock, up to 1.5 m high. *Stems*, inflorescences and petioles patently hairy. *Leaves* sessile or petiolate; blade elliptic, 30–110(–120)  $\times$  10–30(–35) mm, base rounded to subcordate, apex acute, discolorous, upper surface with long, up to 0.75 mm, larged-based, 2-layered setae and much smaller setae in between, orientated  $\pm$  in same direction, lower surface with long setae on midrib and major veins only, intercostal area densely covered with small, bulbous-based setae orientated in different directions; petiole up to 10 mm long. *Flowers* with pedicels up to 30 mm long in fruit. *Calyx* lobes ovate,  $\pm$  9  $\times$  3 mm in flower, 15–18  $\times$  7–9 mm in fruit. *Corolla* very pale blue,

darker at edges of lobes, with reddish purple marks at junction of lobes or lobes with white along mid-area, blue in outer areas; tube funnel-shaped, 5–7 mm long; lobes 5 or 6, broadly ovate,  $\pm 5 \times 1.5$  mm, with abrupt, acuminate apices, usually twisted. *Fruit* of four nutlets; nutlets greyish marble brown, compressed ovoid,  $\pm 4.0$ –4.5 mm long, external face  $\pm$  convex, shiny, internal face 3-angled, rugose. *Flowering time*: January to December.

Although different infraspecific taxa of *T. zeylanicum* have been described, the species does not warrant subdivision in southern Africa. In Australia the species does show differences and three forms are recognizable (Randall 1993).

*Distinguishing characters*: stems, inflorescence axes and petioles patently hairy; leaves discolorous because upper and lower leaf blade surfaces differ in indumentum; calyx lobes 15–18  $\times$  7–9 mm in fruit; apices of corolla lobes acuminate; nutlets smooth, shiny and grey-marbled. *Distribution*: Namibia (Caprivi), eastern parts of the Northern Province, Mpumalanga, Swaziland and northern KwaZulu-Natal (Figure 8); also known from various regions in eastern Africa, the Comoros, Madagascar, the Mascarenes, India, Sri Lanka, Malaya, Java, the Philippines and Australia (Verdcourt 1991), having reached at least some of these areas presumably as a weed of cultivation. *Habitat*: grassland, woodland, in dry river beds, common weed in old and new cultivated land, pioneer in disturbed areas, along roadsides; well-drained sandy, gravelly turf, poorly drained loam or in rocky well-drained soil; full sun. *Illustrations*: Hooker: t. 4820 (1854); Ivens: 83 (1967); Moriarty: t. 103 (1975); Verdcourt: 93 (1991); Bromilow: 157 (1995).

2. *Trichodesma africanum* (L.) Lehm., *Plantae e familia Asperifoliarum nuciferae*: 195 (1818) non R.Br.; C.H.Wright: 11 (1904); F.W.Andrews: 88 (1956); Riedl: 220 (1967); Friedr.-Holzh.: 3 (1967); H.Heine: 323 (1963); Kazmi: 519 (1971); Qaiser: 31 (1979). Type: 'habitat in Aethiopia', *LINN 188.4* (LINN, syn.-PRE, microfiche!).

*Borago africana* L.: 138 (1753). *Pollichia africana* (L.) Medik.: 247 (1783). *Borraginoides aculeata* (L.) Moench: 515 (1794). *Borraginella africana* (L.) Kuntze: 435 (1891).

*Borago verrucosa* Forssk.: 41 (1775). Type: Egypt, Cairo, *Forsskål 288* (C, holo.).

*Borraginoides africana* (L.) Hiern: 721 (1898). Type: Angola, Mossamedes, *Welwitsch 5303* (PRE, syn.!).

Erect, annual or biennial herb, up to 1 m high, harshly scabrid. *Stems* branched, covered with stiff, tubercle-based setae; setae up to 2 mm long. *Leaves* opposite, sessile or petiolate; blade ovate to narrowly ovate, rarely oblong, 50–105(–120)  $\times$  5–30(–80) mm, base auriculate, apex acute, upper surface with setae of different sizes; setae on lower surface stiff, with tubercle-like multicellular bases, mainly on veins; petiole up to 40 mm long. *Inflorescences* terminal at ends of stems and also terminal on lateral branches; flowers with pedicels up to 15 mm long in fruit. *Calyx*: lobes narrowly ovate,  $\pm 6 \times 2$  mm in flower,  $\pm 12 \times 6$  mm in fruit, base truncate to subcordate, apex acuminate, midrib and margins densely hairy with long, stiff setae, setae interspersed with small, fine, simple, unbranched hairs. *Corolla* pale pink when

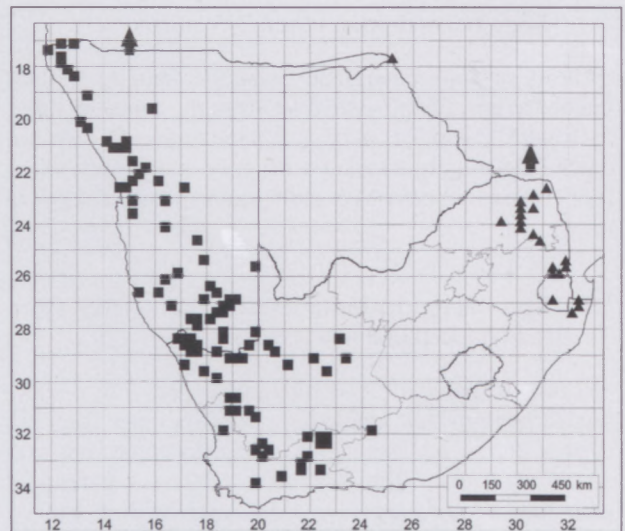


FIGURE 8.—Distribution of *Trichodesma zeylanicum*,  $\blacktriangle$ ; and *T. africanum*,  $\blacksquare$ , in southern Africa.

young, changing to blue, fading white with blue margin, throat yellow with purple spots; tube funnel-shaped, 3–4 mm long; lobes ovate-triangular,  $\pm 2.5$ –3.0 mm long, apices long-acuminate, often twisted. *Fruit* of 4 nutlets; nutlets ovoid-cup-shaped, up to 4 mm long, with glochidia along serrate, raised margins and single ones along midrib, base of cup with thick, short setae and verrucose epidermal protuberances. *Flowering time*: January to December.

*Trichodesma africanum* is a rather plastic species with small leaves and much-branched inflorescences under arid climatic conditions, compared to large leaves and less branched inflorescences when growing in the shade of boulders or during times of above-average rainfall. The different varieties recognized by Brand (1921) and El-Hadidy & Boulos (2000) are not upheld here, but this needs further attention.

*Distinguishing characters*: spinously, patently hairy; leaves variable in size; calyx lobes 12  $\times$  6 mm in fruit; apices of corolla lobes long and acuminate; nutlets ovoid-cup-shaped with distinct serrate, raised margins and a concave, glochidiate inner face. *Distribution*: Namibia, Northern Cape and Western Cape (Figure 8); also known from North and West Africa, Afghanistan, Iran and Pakistan. *Habitat*: disturbed places, road verges, granite or sandstone hills, mountain slopes, among rocks, rocky ridges, dry, sandy river beds, calcareous sandy flats and river banks. *Utilization*: grazed (*Henrici 3393*). *Illustrations*: Heine: 323 (1963); Qaiser: 32 (1979).

3. *Trichodesma angustifolium* Harv., *Thesaurus capensis* 1: 26 (1859); C.H.Wright: 11 (1904); Baker & C.H.Wright: 47 (1905); Brand: 27 (1921); Friedr.-Holzh.: 3 (1967); J.H.Ross: 297 (1972); Brummitt: 852 (1985); Brummitt: 96 (1990); E.S.Martins & Brummitt: 64 (1993); Retief & P.P.J.Herman: 353 (1997); Pooley: 468 (1998). Syntypes: Magaliesberg, *Burke 60, 313* (K, iso.); *Zeyher 1250* (BM, iso.); *Zeyher 1251* (K, iso.); Rhenoster River, Free State, *Sanderson 157* (K, iso.).

*Borraginella angustifolium* (Harv.) Kuntze: 436 (1891).

Perennial herb or subshrub, up to 1.2 m high, with a woody rootstock, appressed hairy throughout, with setae orientated parallel to midrib of leaves. *Stems* erect or decumbent-ascending; setae variable in size or of  $\pm$  equal length; epidermis often flaking off in older plants. *Leaves* shortly petiolate or blades decurrent; blade linear to narrowly elliptic to linear-elliptic, 20–50  $\times$  (1.5–) 3.0–6.0(–15.0) mm, base narrowly cuneate, apex acute, surfaces with setae dense or with spaces in between; petiole up to 3 mm long. *Inflorescences* terminal at ends of main stems and also terminal on lateral branches, lowermost flowers occasionally solitary in leaf axils. *Calyx* setulose, winged,  $\pm$  11  $\times$  4 mm in flower,  $\pm$  25  $\times$  20 mm in fruit, base cordate, apex long-acute. *Corolla* pinkish in young stage, changing to blue or mauve, fading white; tube cylindrical to slightly campanulate,  $\pm$  9–15 mm long; lobes triangular,  $\pm$  5.5  $\times$  4 mm, long-acuminate, often twisted. *Fruit* of 4 nutlets; nutlets glochidiate,  $\pm$  5–6 mm long; glochidia usually coalescing at base to form distinct rim.

**Distinguishing characters:** resprouting perennial, stems, inflorescences and calyces appressed hairy; leaf blades linear to narrowly elliptic; calyx winged,  $\pm$  25  $\times$  20 mm in fruit; nutlets with several-barbed glochidia; glochidia usually coalescing at their bases to form a distinct rim.

#### Key to subspecies

- Indumentum setulose, greyish green; setae well spaced; usually on red, sandy loam; widespread . . . . . subsp. *angustifolium*  
 Indumentum tomentose, silvery grey to greyish green; setae densely packed; usually on lime-rich soils; only known from northern Namibia . . . . . subsp. *argenteum*

#### subsp. *angustifolium*

*Trichodesma lanceolatum* Schinz: 269 (1888). Type: Namibia, Scap River, Schinz 758 (COI!, GRA!, K!, NU!, syn.).

**Flowering time:** October to May. **Distinguishing characters:** indumentum setulose, setae with distinct spaces in between, green; usually on red, sandy loam. **Distribution:** Namibia, Botswana, Northern Province, North-West, Gauteng, Free State, KwaZulu-Natal, Northern Cape (Figure 9); also in Mozambique. **Habitat:** open grassland, open shrubland, mixed shrub savanna, mesophytic closed bush, abandoned lands, disturbed places, mixed ruderal vegetation; red sandy loam, stony soils; plants reach a considerable age and large rootstocks may be more than a century old. **Common name:** blue-bells, according to Smith (1966); 'mothlagapele' (Moss BMP735). **Medicinal use:** dried ground root powder mixed with cold water is used for diarrhoea (Moss BMP735). **Illustrations:** Harvey: t. 40 (1859); Pooley: 469 (1998).

subsp. *argenteum* Retief & A.E.van Wyk, subsp. nov., subsp. *angustifolio* affinis sed foliis dense pilosis (non intervallis conspicuis inter bases setarum), plerumque in solo calcareo, non luto arenoso rubro habitat.

**TYPE.**—Namibia, 1916 (Gobaub): Etosha National Park, between Gemsbokvlakte and Olifantsbad, (–AA), Retief 1404.01 (PRE, holo.; WIND).

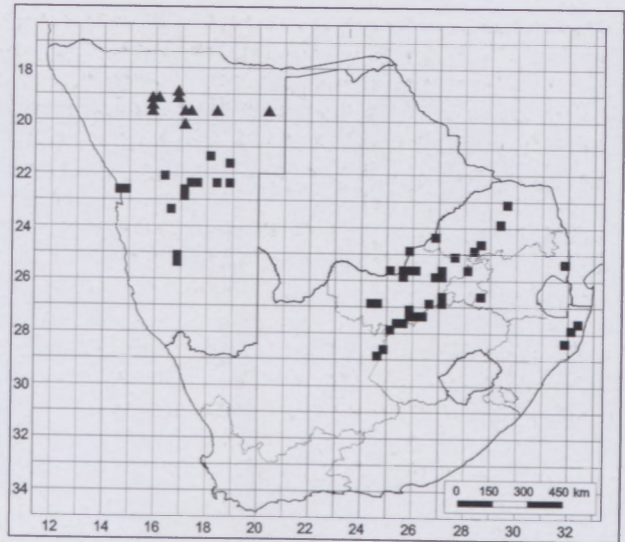


FIGURE 9.—Distribution of *Trichodesma angustifolium* subsp. *angustifolium*, ■; and *T. angustifolium* subsp. *argenteum*, ▲, in southern Africa.

The prominent silver-grey to greyish green indumentum is reflected in the specific epithet: 'argenteum' = silver. The difference in the density of the setae on the leaf surfaces, distinguishes the two subspecies. This distinction is further supported by habitat differences.

**Flowering time:** November to April. **Distinguishing characters:** indumentum tomentose, silvery grey to greyish green; setae densely packed; usually on lime soils. **Distribution:** northern part of Namibia (Figure 9). **Habitat:** grassland, savanna, margins of pans, road verges; usually in grey, lime-rich soils.

4. *Trichodesma physaloides* (Fenzl) A.DC., Prodrum 10: 173 (1846); Gürke: 99 (1897); C.H.Wright: 11 (1904); Baker & C.H.Wright: 46 (1905); Brand: 22 (1921); Pole Evans: t. 351 (1929); Letty: 280 (1962); Taton: 39 (1971); Agnew: 521 (1974); Brummitt: 439 (1982); Brummitt: 96 (1990); Verdc.: 100 (1991); E.S.Martins & Brummitt: 65 (1993); Germish. in A.Fabian & Germish.: 338 (1997). Retief & P.P.J.Herman: 353 (1997); A.E.van Wyk & C.E.Malan: 46 (1997); Pooley: 178 (1998). Type: Sudan, Fazokl, Kotschy 577 (BM, K!, iso.).

*Friedrichsthalia physaloides* Fenzl: 54 (1839). *Boraginella physaloides* (Fenzl) Kuntze: 435 (1891).

*Trichodesma droogmansianum* De Wild. & T.Durand: 69 (1900). *T. droogmansianum* De Wild. & T.Durand var. *glabrescens* (Gürke) Brand: 24 (1921). Type: Zaïre, Lualaba, Descamps s.n. (BR, holo.).

*T. glabrescens* Gürke: 389 (1901). Type: Tanzania, Kinga-Berge, Ussangu, Goetze 1267 (BR, E, iso.–K, photo.!).

*T. ringoetii* De Wild.: 100 (1914). Type: Zaïre, Katanga, Nieuw-dorp, Ringoet 6 (BR, holo.).

Perennial herb with 1 to several annual stems from a woody rootstock, up to 0.5 m tall. *Stems*  $\pm$  glabrous, with scattered setae; young stems fleshy, pinkish. *Leaves* sessile, bluish green; blade broadly ovate to narrowly ovate, 30–50(–75)  $\times$  12–16(–32) mm, base cuneate to rounded, apex acute or obtuse, upper surface clothed with short,

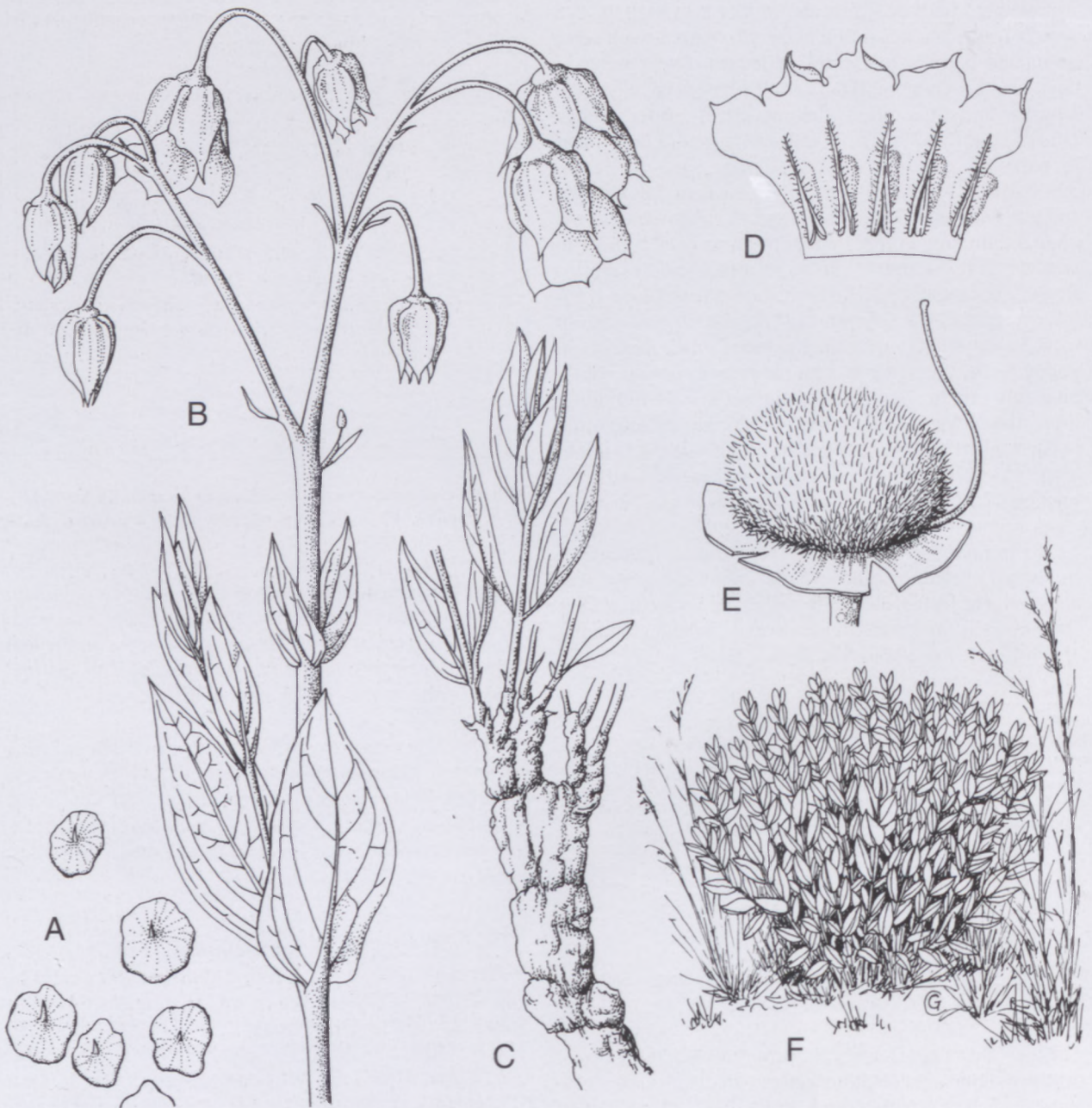


FIGURE 10.—*Trichodesma physaloides*, Germishuizen 2156 (PRE). A, setae on upper surface of leaf,  $\times 23$ ; B, flowering stem,  $\times 1$ ; C, rootstock with young shoots,  $\times 1$ ; D, longitudinal section of corolla,  $\times 1.5$ ; E, nutlet,  $\times 3$ ; F, habit reduced, plant in Pretoria National Botanical Garden. Artist: Gillian Condy.

stiff setae; setae all pointing  $\pm$  in same direction, multicellular base discoid, 3–5-layered; lower surface with scattered setae on midrib and veins only. *Inflorescences* terminal, cymose panicles, cymules scorpioid; pedicels up to 30 mm long, drooping. *Calyx* brownish purple; lobes 13–15  $\times$  5–7 mm in flower, up to 30  $\times$  18 mm in fruit. *Corolla* white with brown gibbositities at sinuses between lobes, apices of lobes with a light brown rim; tube funnel-shaped, hairy inside at level where anthers arise; lobes broadly ovate, apices cuspidate, glabrous or densely pilose down middle of lobes on adaxial side. *Fruit* one discoid nutlet; nutlet with a prominent rim, densely hairy, with style and stigma lateral due to abortion of three other nutlets. *Flowering time*: August to November. Figure 10.

*Distinguishing characters*: multistemmed greyish green suffrutex; stems glabrous or with setae with promi-

nent discoid, multicellular bases; flowers drooping; calyx brownish purple; corolla white with a light brown rim at apices of lobes; fruit a hairy, discoid nutlet. *Distribution*: Northern Province, North-West, Gauteng, Mpumalanga, Swaziland, KwaZulu-Natal (Figure 11); also known from southern Sudan, western Ethiopia, Kenya, Uganda, Burundi, Tanzania, Zaïre, Zambia, Malawi, Zimbabwe and Mozambique. *Habitat*: grassland, woodland, open mixed bushveld, hill slopes, disturbed areas, roadsides, waste places; sandy loam, clay, loam or rocky soils, gravel; large plants may have rootstocks well over a century old. *Common name*: chocolate bells. *Illustrations*: Pole Evans: t. 351 (1929); Letty: t. 139, 3 (1962); Moriarty: t. 30 (1975); Brummitt: 431 (1982); Onderstall: 167 (1984); Brummitt: 97 (1990); Fabian & Germishuizen: 339 (1997); Van Wyk & Malan: 47 (1997); Pooley: 179 (1998).

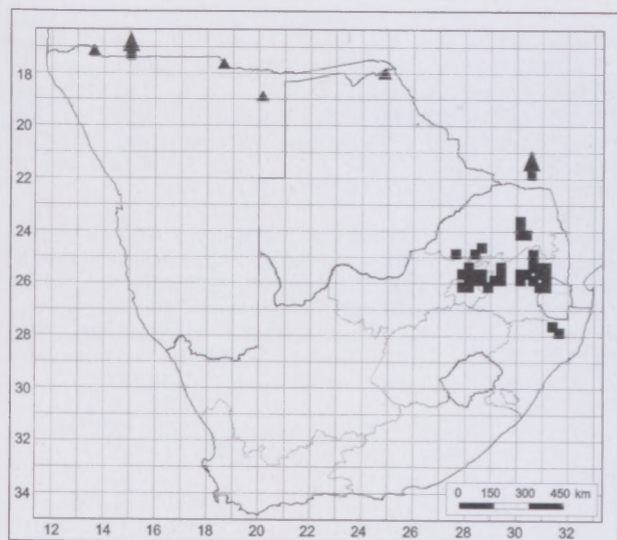


FIGURE 11.—Distribution of *Trichodesma physaloides*, ■; and *T. ambacense* subsp. *hockii*, ▲, in southern Africa.

5. *Trichodesma ambacense* Welw. in Annaes do Conselho ultramarino 1: 589 (1859) as '*ambacensis*'; Brummitt: 442 (1982); Brummitt: 98 (1990); Verdc.: 101 (1991). *Boraginella ambacensis* (Welw.) Kuntze: 435 (1891). *T. angolense* Brand: 26 (1921), nom. superfl. illegit. Type: as for *T. ambacense* above. Type: Angola, Welwitsch 5450 (LISC, holo.; BM, BR, COI!, K!).

Currently *T. ambacense* is divided into two subspecies (Brummitt 1982). *T. ambacense* subsp. *ambacense* is endemic to Angola. It differs from subsp. *hockii* in the leaves which are obovate to oblanceolate (not ovate to elliptic) and calyx lobes which are 3–5 mm long in flower (not 5–8(–9) mm long).

subsp. *hockii* (De Wild.) Brummitt in Kew Bulletin 37: 443 (1982); Roessler: 39 (1984); Brummitt: 98 (1990); Verdc.: 101 (1991); E.S.Martins & Brummitt: 67 (1993); E.S.Martins: 5 (1993); Bolnick: 32 (1995). Type: Zaïre, Shaba, Lubumbashi [Elisabethville], Hock (BR, holo., –K, photo.!).

*Trichodesma hockii* De Wild.: 546 (1913).

*T. ledermannii* Vaupel: 529 (1912). Type: Cameroon, near Laro, Ledermann 3080 (B, holo.†).

*T. tinctorium* Brand: 393 (1914). Type: Zaïre, Shaba, Lukafu, Verdick 104 (BR, holo.).

*T. verdickii* Brand: 329 (1914). Type: Zaïre, Shaba, Lukafu, Verdick 140 (BR, holo.).

Perennial herb with annual stems from a woody rootstock, up to 0.5 m high. Stems hairy or setose. Leaves sessile or occasionally shortly petiolate; blade ovate to elliptic, 50–65 × 20–27 mm, base cuneate, apex acute; petiole up to 1.5 mm long. Inflorescences terminal at ends of stems, cymose panicles, cymules scorpioid; flowers slightly pendent; pedicels up to 25 mm long in fruit. Calyx ± 14 × 8 in flower, ± 22 × 15 mm in fruit. Corolla deep blue, pale lavender to white with raised amber-brown gibbositities at sinuses of petal lobes; tube campanulate, lobes reflexed, apices acuminate. Fruit:

one, densely silken-haired nutlet; hairs usually hooked. Flowering time: June to September.

*Distinguishing characters*: multistemmed suffrutex; stems hairy; leaf blade elliptic; setae with prominent discoid, multicellular bases, usually hooked at apices; flowers slightly pendent; corolla deep blue, lobes reflexed; fruit a silken-haired nutlet. *Distribution*: Namibia, Botswana (Figure 11); also known from Sudan, Nigeria, Cameroon, Uganda, Kenya, Tanzania, Zambia, Malawi, Mozambique and Zimbabwe. *Habitat*: grassland, woodland, abandoned fields, roadsides; sandy soil. *Common name*: bells of St Mary's. *Illustrations*: Moriarty: t. 103 (1975); Martins & Brummitt: 69 (1993); Bolnick: t. 15 (1995).

SPECIMENS EXAMINED (southern Africa only)

Numbers in brackets signify the identity of the specimens: (1) *Trichodesma zeylanicum*; (2) *T. africanum*; (3a) *T. angustifolium* subsp. *angustifolium*; (3b) *T. angustifolium* subsp. *argenteum*; (4) *T. physaloides*; (5) *T. ambacense* subsp. *hockii*.

Acocks 1541 (3a) PRE; 1619, 18133 (3a) K, PRE; 2026, 2533 (2) BOL, K, PRE; 2578 (3a) BOL, PRE; 2587 (3a) K. Acocks & Hafström 1314, 1350 (2) PRE; 1315 (4) PRE. Adamson D147 (2) PRE. Anderson N18 (3a) PRE.

Balkwill 1499 (1) NU, PRE. Balkwill & Cadman 3501 (4) E, PRE. Balsinhas 3014 (3a) K, PRE. Balsinhas & Kersberg 2006 (2) PRE, WIND. Barber s.n. (3a) K; PRE13748 (3a) PRE. Barker 102 (4) J; 791 (3a) PRE. Barnard SAM36092 (2) SAM. Barrett 132 (1) K, PRE. Bengis 463 (2). Bolus 641 (2) BM, BOL, K; 5713 (3a) K; 6443 (3a) BOL, PRE; 9706 (4) BOL; 10399 (2) BOL. Bond 842 (2) NBG. Boshoff & Mason 2541 (3a) PRE. Boss 18, A80, TRV35550 (3a) PRE; TRV36168 (2) PRE. Botha & Ubbink 1733 (3a) PRE. Boucher 5147 (2) NBG. Bradfield 583 (2) K, PRE. Bremekamp TRV27519 (1) PRE. Breyer PRE59361, TRV17580 (1) PRE; PRE59405, TRV20582 (3b) PRE. Brown & Kolberg 277 (3b) WIND. Bryant J118 (2) PRE; 894B (2) K. Buchanan sub Wood 7032 (4) PRE. Buitendag 626 (4) K, PRE. Burchell 1264 (2) K, PRE. Burger & Louw 297 (2) NBG, PRE. Burgoyne 408 (4) PRU. Burke 60, 313 (3a) K; PRE13749 (4) PRE. Burt Davy 2051 (4) PRE; 7048 (3a) K; 11009, 11278, 14393 (3a) NBG.

Catell 314 (2) NBG. Chennells 151 (3a) BOL, PRE. Clarke 22/57 (1) PRE; 1318 (4) PRE. Codd 627 (4) PRE; 2084, 6645 (3a) K, PRE. Cole 1388 (3a) PRE. Comins 663 (2) K, PRE; 1801 (2) PRE. Compton 2447, 11530, 20616 (2) NBG; 27100 (4) K, PRE; 28934 (1) NBG, PRE. Craven 14, 184, 216, 1556, 1939, 3136 (2) WIND. Crook M37, 737 (4) PRE. Crosby 863 (2) PRE. Cross 228 (4) PRE.

Davidse 6285 (2) PRE. Davies, Thompson & Miller 48, 104 (2) PRE, WIND. De Kruij 1231 (4) PRE. De Lange UNIN6718 (4) PRE, UNIN. De Sousa 559 (4) PRE. De Winter 419 (5) BM, K, PRE; 2473 (3a) K, PRE, WIND. De Winter & Giess 6158 (2) K, PRE, WIND. De Winter & Leistner 5685 (2) K, PRE, WIND. Dean 325 (2) BOL, PRE. Dinter 415 (3a) K, SAM; 925 (3b) NBG; 1213, 1273 (2) SAM; 3503 (3a) K, PRE; 4296 (3a) BM, SAM; 4799 (2) K; 8423 (3a) BM, K. Dlamini PRE40761 (4) PRE. Drège s.n. (2) K. Drèyer 52 (2) PRE. Du Plessis 814, 1046 (4) PRE, PRU; 3100 (4) K, PRE.

Edwards PRE40742 (4) PRE. Elan-Puttick 292 (4) PRE. Esterhuysen 2712 (2) NBG, PRE; 4488 (2) BOL. Evrard 9034, 9243 (2) PRE.

Fourie 2804 (4) PRE. Francois 45 (4) E. Fries, Norlindh & Weimarck 1966 (4) PRE. Fuller PRE10596 (4) BM.

Galpin 502M, 503M (3a) PRE; 504M, 6994 (4) PRE; 9223 (1) PRE; 9288 (4) K, PRE; 11380 (1) K, PRE; 13700 (3a) K, PRE; 14111 (2) BOL, K, PRE; 15097 (5) E. Galpin s.n. (4) K. Galpin & Pearson 1561 (2) BOL; 7506 (2) K, PRE, SAM. Germishuizen 2156 (4) K, PRE; 3086 (4) PRE; 4575, 5377, 5431 (2) PRE. Gerstner 3435 (4) NH; 4101 (3a) NH; 5119 (4) K, PRE; 5133 (3a) PRE; 6616 (1) PRE. Gibbs

- Russell, Robinson & Herman 311 (2) PRE. Giess 3628 (2) WIND, 8033 (2) PRE. WIND; 8311 (3a) PRE, WIND; 9488 (5) WIND; 10700 (3a) WIND; 1331 (5) PRE. WIND. Giess & Loutit 14101 (3b) K. PRE. WIND. Giess & Müller 11980 (2) K. PRE. WIND. Giess & Van Vuuren 947 (3a) K. PRE. WIND. Giess & Wiss 3295 (2) WIND. Giess, Volk & Bleissner 6276 (2) WIND; 6512 (3b) WIND. Gillet 2599 (3a) K; 4625 (4) K. Goldblatt 1986 (2) PRE. WIND; 2349A (2) NBG, PRE; 7003 (2) PRE. Goosens PRE40757 (4) PRE. Greenway 8113 (4) PRE. Greuter 21604, 21802 (2) PRE. Gubb 32.92 (3a) PRU.
- Hall 57, 74 (1) NBG; 400, 798 (2) NBG. Harris 127 (4) PRU. Hanekom 1498 (3a) K, PRE; 1619 (3a) K; 2151 (2) K. PRE. Hansen 3277 (3a) PRE. Hardy 1950 (2) K. WIND; 2470 (2) K. PRE; 5656 (1) K, PRE. Hardy & Bayliss 1239 (3a) K. PRE. Hardy & De Winter 1393 (2) PRE. Hardy & Venter 4565 (2) K. PRE. WIND. Henrici 74 (3a) PRE; 3393 (2) PRE. Heymans 13 (4) J. Hill PRE40760 (3a) PRE. Hilliard 4731 (1) NU. Hillary & Robertson 601 (3a) PRE. Hines 400 (3b) WIND. Hutchins 319 (1) PRE. Hoffmann 1233 (2) NBG. Holt 8 (4) NH. PRE. Homann, Benseler & Mittendorf 22 (2) WIND. Howlett PRE40752 (4) PRE. Hugo 505, 2533 (2) K, NBG, PRE. Hutchinson 2987 (3a) BM, BOL, K, PRE. Hutchinson & Gillett 3590 (5) COI.
- Ihlenfeldt, De Winter & Hardy 3226 (2) PRE. Immelman 569 (3a) PRE. WIND; 579 (2) PRE.
- N. Jacobsen 1813 (4) PRE. W.J. Jacobsen 1059 (3a) PRE. JBG6154 (4) PRE. Jeffers 414 (3a) PRE. Jenkins 7432, 9130, TRV9130 (4) PRE; 7538 (3a) PRE; TRV8185 (1) PRE. Jensen 49, 70, 195, 241, 281, 1395 (2) WIND. Joffe 332 (4) PRE. Joubert 100/1447 (3b) WIND. Junod 548 (1) K, PRE; 604 (4) K; 5022 (1) E; 604 (4) K, PRE.
- Karsten PRE31340, PRE31341 (4) PRE. Kers 7062, WIND26641 (2) WIND. Killian 20 (1) K, PRE. Kinges 1851 (4) PRE; 2305, 2399 (2) PRE. WIND. Kluge 113 (4) PRE. PRU. Koch A15 (2) PRE. Kok 265 PRE, PRU; 1046 (4) PRU. Kraeusel & Wiss 1913 (2) WIND. Krynauw 70 (3a) PRE; 1283 (4) PRE. Kubirske 186 (2) K. Kubirske, Strohbach & Swart 186 (2) WIND.
- La Croix 3339, 4874 (4) PRE. Laidler 662 (2) NBG, PRE. Lang TRV32136 (1) PRE. Lavranos 11019 (2) PRE. Lavranos & Phelemann 20148 (3a) WIND. Lea 43 (4) PRE. Leendertz 267, 360, 824 (4) PRE. Le Roux 13 (4) PRE, 483 (3b) PRE. WIND; 3064 (2) NBG. Leach & Bayliss 13067 (2) K, PRE, WIND. Leeman PRE40744 (4) PRE. Leendertz 267, 300, 824, 7594 (4) PRE; 713A, 8519, TRV11437 (3a) PRE. Leistner 1240 (3a) K, PRE; 2338 (2) K, PRE. Leistner & Joynr 2846 (2) PRE. Leistner, Oliver, Steenkamp & Vorster 139 (2) K, PRE. Leuenberger, Raus & Schiers 3266 (2) WIND. Levyns 1742 (2) BOL. Liebenberg 5008 (2) PRE, WIND; 5103 (3a) WIND; 5158 (2) K, PRE. WIND; 5703 (3a) PRE. Lloyd 35, 36 (2) PRE. Louw 2029 (3a) PRE.
- MacCallum 541, 1589 (4) PRE. MacDonald 97, 357, 490, 568 (2) BM; 383 (3a) BM. Maguire 365 (2) NBG. Malan 9 (1) PRE. Mathibe 64 (4) PRU. Matthews 230 (2) PRU. Methuen 166 (4) PRE. Miller 2489 (4) PRE. Marloth 780 (3a) PRE; 1188 (2) NBG; 1411, 2034 (2) PRE; 10162 (4) PRE; 12380 (2) NBG, PRE. McMurry 4100, 10773, 15325, 19179, 23918 (4) J. Meebold SAM51370 (1) SAM. Merxmüller 739, 1669 (2) PRE. WIND; 1325 (3b) K. PRE. Merxmüller & Giess 1325 (3b) WIND; 1669 (2) WIND; 2827, 28107 (2) PRE. WIND. Mogg 8176 (3a) PRE. SAM; 8363, PRE11704, SAM44701 (3a) PRE; 9450 (4) SAM; 15325, PRE9449, PRE10773 (4) PRE; 19179, 23918 (4) J. Moore 44 (3a) PRE. Moran PRE40756 (3a) PRE. Morris & Engelbrecht 1135, 1155 (3a) K. PRE. Moss BMP735 (3a) PRE; 4736, 22227 (4) J; 8855 (4) BM, J. Moss & Jacobsen K218 (2) PRE. Müller 29 (3a) PRU, WIND; 124 (2) PRE. WIND; 781 (3a) PRE; 1290 (3a) PRE. WIND. Müller & Loutit 1198 (2) WIND. Murray 614 (3a) PRE; 641 (4) PRE. Myre 21 (1) PRE.
- Nation 288 (3a) K. Nelson 236 (3a) PRE. Netshungani 915 (1) PRE. Nicholas 2576 (2) PRE. WIND.
- Obermeyer 711 (1) PRE; NH27321 (4) NH; TRV34735 (4) BM, PRE. Oliver & Steenkamp 6291 (2) K. PRE. WIND. Oliver, Tölkén & Venter 89 (2) K, NBG, PRE. Onderstall 443, 1248 (4) PRE.
- Pager P35 (2) WIND. Papendorf 375 (1) PRE. Parry PRE8016 (1) PRE. Patterson 21 (1) PRE. Pearson 3665 (3a) BOL, K, PRE. SAM; 3674 (3a) K, PRE; 4961 (2) K, NBG, PRE; 4993, 6005 (2) K; 6106 (2) BM, K; 8551, 9123 (2) BOL, K; 9110, 9531 (3a) BOL, K. Peeters, Gericke & Burelli 163 (3a) PRE. Pegler 979 (3a) BOL, K, PRE. SAM.
- Peyper 1333 (3a) PRE. E. Phillips 1117 (4) J; 3275 (4) J, PRE. J. Phillips 1616 (4) PRE. Phillips & Liebenberg 916 (3a) PRE. Phipps 778 (4) PRE. Pienaar 1089 (2) BOL, PRE. Pienaar & Vahrmeijer 478 (1) PRE. Pillans 5074 (2) BOL, K; 5856 (2) BOL. Plowes 7046 (3a) PRE. Pole-Evans 2827 (5) PRE; s.n. (4) K; PRE40746 (4) PRE; PRE12870, PRE13241, PRE40765 (3a) PRE. Pont 512 (3a) PRE. Potts BLFU2676 (3a) BLFU. Pooley 435 (3a) NU; 524 (1) NU. Prosser P1071 (4) K, PRE; J029438 (4) J; JBG1204 (4) PRE.
- Range 1030 (3a) SAM. Rehmann 4522 (3a) BM. BOL; 4759 (4) BM. BOL. Repton 283 (4) PRE; 3410 (3a) K, PRE; UNIN4540 (4) PRE. Retief 1404.01 (3b) PRE. WIND; 2223, 2224 (4) PRE. Roberts PRE15862 (4) PRE. Rodin 2862 (3a) BOL, K; 3657 (3a) BOL, K, PRE. Rogers 5039, 22270 (3a) PRE; 8290 (4) BOL; 13453 (1) PRE; 15322 (2) K; 18123 (1) K; 21405 (4) SAM; 22072, TRV26665 (4) PRE. Rösch & Le Roux 109, 179 (2) PRU, WIND. Rusch 45 (2) WIND.
- SAGP/SAAB 1/76 (4) K, PRE. PRU. Sanderson 157 (3a) K. Scheepers 349 (1) K, PRE. PRU, UNIN; 1166 (4) BM, K, PRE. PRU; 1616 (3a) PRE. Schenck 49 (3a) PRE. Schinz 758 (3a) COI, GRA, K, NU. Schlechter 3601 (4) BM, E, J, PRE; 3677 (3a) BM, BOL, K, PRE; 5365 (3a) PRE; 10871 (2) BM, BOL, COI, K, PRE. Schlieben 8996 (2) BM, K, PRE. Schmidt 295 (2) PRE. WIND. Schoenfelder 227 (3a) PRE. Schulze 8 (1) PRU. Schweickerdt 1102 (3a) PRE. Schwerdtfeger 4181 (3a) WIND; 4286 (2) WIND. Seely 2009 (2) WIND. Seely & Robinson 306 (2) WIND. Seely & Ward 8, 9 (2) WIND. Seydel 314 (2) K; 1845 (3a) WIND; 1847, 2074 (3a) K; 2076 (3b) WIND; 1049, 2470, 4049 (3a) K, PRE, WIND; 2971, 4334 (2) K. Shearing 115, 620, 1083 (2) PRE. Sim 20638 (1) PRE. Smit 1759 (4) PRU. Smith 153, 875, 1082A, 1215, 2131, 3250 (3a) PRE; 821, 837 (4) PRE. Smook 7695, 8691 (2) PRE. Smook & Harding 713 (2) K, PRE. Smuts & Gillett 3290 (4) PRE. Snyman C (1) PRE. Stalmans 158, 1408 (4) PRE; 1076 (1) PRE; 1996 (1) J. Steiner 624 (2) NBG. Stewart TRV8883 (4) PRE; 8966 (3a) PRE; 8970 (1) PRE. Stohr 219 (4) BOL. Story 758 (3a) PRE; 1361 (4) PRE; 5745 (2) K, PRE. Strey 2020 (2) BOL, PRE; 2153 (3a) K, PRE; 6588 (1) K, NU, PRE; 7890 (1) PRE. Strohbach 29 (2) WIND. Sutton 228 (3a) PRE.
- Taylor 3396 (1) NBG; 3462B, 11537 (2) NBG. Theiler PRE59972 (3a) PRE. Theron 1517 (4) PRE, PRU; 3899 (2) PRU. Thode 4764, 4766 (3a) PRE; A1453 (3a) K, PRE. Thorncroft TRV4550 (4) PRE; NH11609 (4) NH. Thorne SAM51582 (2) SAM. Tinley 1108 (3b) PRE. WIND. Tölkén & Hardy 717 (3a) K, PRE, WIND. Trapnell 507 (4) K. Tuck 813 (3a) BOL, SAM; 2213 (3a) BM.
- Ubbink 744, 1141 (3a) PRE. Ueckermann 7295 (2) PRE.
- Van Breda 4009, 4331, 4416 (2) PRE. Van Dam PRE59662, TRV25002 (1) PRE. Van der Schijff 542 (1) KNP, PRE; 3132 (1) K, KNP, PRE; 5952 (1) PRU; 8195 (2) PRE, PRU. Van Hoepen 1952 (2) BOL. Van Jaarsveld 1496, 2529, 8413, 11921 (2) NBG; 8825 (2) NBG, PRE. Van Rooyen 2017 (4) K, PRE, PRU; 2268 (2) PRU. Van Wyk 707 (2) PRE; 734 (3a) PRE; 1748 (4) PRE; 3803 (1) PRE, PRU; 6582 (2) PRE, PRU; 8578A (2) PRE, PRU, WIND; 8595 (2) PRE, PRU; 8778 (2) PRE, PRU, WIND; 12682 (1) PRU. Vinjevold CV11 (2) WIND. Visser 210 (2) PRE, PRU. Vlok 1491 (2) PRE. Volk 867 (3a) PRE; 2465A (2) PRE. Von Koenen 559, WIND26672 (3a) WIND.
- Wallich 1847, s.n. (4) K. Walter 981 (3b) WIND. Wanntrop 676 (3a) PRE; 979 (2) K, PRE. Ward 2596 (1) PRE; 3216 (3a) K, NU, PRE; 12614 (1) NU. Wasserfall 1098 (2) K, PRE. Walmough 866 (2) PRE. Way PRE31343 (4) PRE. Wells 2217 (3a) K, PRE. Wendt 25/4, 32, 85, 2616, C/20, sub Giess 13614, sub Giess 14762 (2) WIND. Werdermann & Oberdieck 587 (2) PRE; 2331 (3b) K, NBG, PRE. Wild 3331 (1) PRE. Williams 169 (4) E. Williamson 3958, 5562 (2) NBG. Wilman PRE40755 (3a) PRE. Wilms 943 (3a) BM, K, Wiss 1944 (2) WIND. Wood 7002 (4) PRE. Worsdell s.n. (3a) K.
- Young A190 (4) PRE.
- Zeyher 98 (4) SAM; 1239 (2) BM, K, SAM; 1249 (4) K, PRE, SAM; 1250 (3a) BM; 1251 (3a) BM, K, SAM. Zietsman 1747 (2) WIND; 2100 (2) PRU. Zinn SAM63451 (2) SAM.

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