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

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**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 twisted 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.

INTRODUCTION

Brown described *Trichodesma* in 1810, a genus well defined by flowers with a deeply divided and strongly accrescent calyx, the absence of fomices, 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 represented 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.

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 Erdtmann (1960).

HISTORICAL OUTLINE

Brown (1810) based his concept and description of *Trichodesma* on *Borago zeylanica* Burm.f. and *B.
africanaum L. When De Candolle (1846) revised the genus, he recognized eight species. In the description of *T. africanaum*, Jean-Baptiste Denis 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 physalooides* Fenzl, a species previously described from the Sudan.

Wright (1904) noted that *T. physalooides* (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. africanaum* 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. africanaum*, *T. angustifolium*, *T. arenicola* Gürke, *T. physalooides*, 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. africanaum* (L.) Lehman., *T. ambacense* Welw. subsp. **hockii** (De Wild.) Brummitt, *T. angustifolium* Harv. subsp. **angustifolium**, *T. angustifolium* Harv. subsp. **argentatum** Retief & A.E. van Wyk subsp. nov., *T. physalooides* (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. africanaum*, 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. physalooides* 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 fomices 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 plicate (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. africanaum* 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 *Afrotysomia*. The types of glochidia found in *Trichodesma*, however, differ from those of *Cynoglossum* and *Afrotysomia*. Hilger (1985) studied the development and morphology of flowers and fruits of 23 species of the *Cynoglossaeae* and *Ehrteiaceae*, and commented on the implications of his findings on the taxonomy of these groups. He found that in most *Cynoglossaeae* the nutlets are initially positioned with their disc (the flat base) parallel to the basal area (the nectary disc) of the gynoeicum. 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* Savir 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 Trigonotidieae (Riedl 1997). *Suchtelenia* has 6-heterocolpate pollen grains, showing similarity to pollen of members of *Heliotropioideae*, *Cynoglosseae*, *Ehrteiaceae* and *Myosotideae*. The triaperturate pollen grains of *Trichodesma* and *Caccinia*, on the other hand, show similarity to pollen of the subfamilies *Wellstedioideae* and *Ehretiaceae*. The tribe *Trichodesmeae* can be regarded as 'primitive' within the subfamily *Boraginaeae*, showing similarities to various other genera within the *Boraginaeae s.l.* The family is sometimes treated as two separate entities, *Boraginaeae s. str.* and *Ehretiaceae*, but various characteristics support the recognition of one family divided into several subfamilies (Retief & Van Wyk 1999a).

**MORPHOLOGICAL CHARACTERS OF TAXONOMIC SIGNIFICANCE**

**Habit**

*Trichodesma* is a genus of perennial and annual herbs or subshrubs. *T. africanaum* 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**

Infraspecific 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 ± 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.

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

(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 dispersal 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
study, a finding that is in agreement with Brummitt (1982). Pollen grains of the genus are isopolar, radially symmetrical, tricolporate, subspheroidal, with $P = 7.0-11.5 \mu m$, $E = 6.0-9.5 \mu m$, $P/E = 1.1-1.2$ (Figure 5A–F). The shape of the pollen grains in polar view is ± 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 lalongate (Figure 5D). The tectum is nodular with nodules ± 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.
Bothalia 32,2 (2002)

FIGURE 4.—Trichodesma physaloides. Mature fruit and accrescent calyx, × 1. Retief 2223 (PRE).

ambacense subsp. hockii (sect. Friedrichsthalia (Fenzl) A.DC.) are characterized by a single, ± 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 6f).

**PHYTOGEOGRAPHY**

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

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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* 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**


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, planovex or biconvex, smooth or variously ornamented.

The name *Trichodesma* alludes to the twisted hairs or awns that terminate the anthers; Greek *thriz, 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 ± winged margin; nutlets compressed-ovoid, outer face usually mottled with grey and brown, inner face rugose, covered with indistinct papillae (T. zeylanicum).


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 glocidiate; gynobase pyramidal with four strongly concave sides, each with ± winged margin, verrucose (T. africanum).

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 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. africannum

3b Glochidia slender, covering whole surface of nutlet; leaf blade linear to narrowly elliptic, lower and upper surfaces 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 scattered on midrib and veins, upper leaf blade covered with similar setae well spaced .............................................. 4. T. physaloides

4b Corolla lobes blue or rarely whitish, ± triangular, with long acute apices; lower leaf blade surface covered with long and much smaller setae in between, orientated ± 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 .............................................. 1. T. zeylanicum


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

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

Erect, perennial herb with annual stems from a woody rootstock, up to 1.5 m high. Stems, inflorescences and petals pale yellow. Leaves sessile or petiolate; blade elliptic, 30–110–120) 10–30–35) mm, base rounded to subcordate, apex acute, discolorous, upper surface with long, up to 0.75 mm, large-based, 2-layered setae and much smaller setae in between, orientated ± 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, ± 9 × 3 mm in flower, 15–18 × 7–9 mm in fruit. Corolla very pale blue.
darkness 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, ± 5 × 1.5 mm, with abrupt, acuminate
apices, usually twisted. Fruit of four nutlets; nutlets grey-
ish marble brown, compressed ovoid, ± 4.0–4.5 mm long,
external face ± 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 subdi-
vision in southern Africa. In Australia the species does
show differences and three forms are recognizable (Randall 1993).

Distinguishing characters: stems, inflorescence axes
and petioles patent hairy; leaves discolorous because
upper and lower leaf blade surfaces differ in indumentum;
calyx lobes 15–18 × 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, Mpmalanga, Swaziland and north-
ern KwaZulu-Natal (Figure 8); also known from various
regions in eastern Africa, the Comoros, Madagascar, the
Mascarénes, 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, pio-
neer 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);

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 verrucosa Forssk.: 41 (1775). Type: Egypt, Cairo, Forsskål
288 (C, hol.).

Borrainioides africana (L.) Hier: 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, ses-
sile or petiolate; blade ovate to narrowly ovate, rarely
oblanceolate, 50–105–(120) × 5–30–80 mm, base auriculate,
apex acute, upper surface with setae of different sizes;
setae on lower surface stiff, with tubercle-like multicellu-
lar bases, mainly on veins; petiole up to 40 mm long.
Inflorescences terminal at ends of stems and also termi-
nal on lateral branches; flowers with pedicels up to 15
mm long in fruit. Calyx: lobes narrowly ovate, ± 6 × 2
mm in flower, ± 12 × 6 mm in fruit, base truncate to sub-
cordate, apex acuminate, midrib and margins densely
hairless with long, stiff setae, setae interspersed with small,
fine, simple, unbranched hairs. Corolla pale pink when

young, changing to blue, fading white with blue margin,
throat yellow with purple spots; tube funnel-shaped, 3–4
mm long; lobes ovate-triangular, ± 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
glomeroidial late serra, raised margins and single ones
along midrib, base of cup with thick, short setae and ver-
rusic 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 bushes or during times of above-average rainfall.
The different varieties recognized by Brand (1921)
and El-Haddy & Boulos (2000) are not upheld here, but this
needs further attention.

Distinguishing characters: spinously, patent hairy;
leaves variable in size; calyx lobes 12 × 6 mm in fruit;
apices of corolla lobes long and acuminate; nutlets
ovidoid-cup-shaped with distinct serra, 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).

3. Trichodesma angustifolium Harv., Thesaurus
Plantarum 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). Synotypes: Magaliesberg, Burke 60, 313 (K,
iso.!!); Zeyher 1250 (BM, iso.!!); Zeyher 1251 (K, iso.!!);
Rhenoster River, Free State, Sanderson 157 (K, iso.!!).

Borrainiella angustifolium (Harv.) Kunze: 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 ± 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 × (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, ± 11 × 4 mm in flower, ± 25 × 20 mm in fruit, base cordate, apex long-acute. Corolla pinkish in young stage, changing to blue or mauve, fading white; tube cylindric to slightly campanulate, ± 9–15 mm long; lobes triangular, ± 5.5 × 4 mm, long-acuminate, often twisted. Fruit of 4 nutlets; nutlets glochidiate, ± 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, ± 25 × 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, 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, savanna, margins of pans, road verges; usually in grey, lime-rich soils.

**subsp. argenteum** Retief & A.E. van Wyk, subsp. nov., subsp. angustifolium affinis sed foliis dense pilosis (non intervallis conspicuis inter bases setatum), pleuroquene in solo calcareo, non luto arenoso rubat habitat.

**TYPE.**—Namibia, 1916 (Gobaub): Etosha National Park, between Gembokvlakte 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.](image)

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.


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

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

*Trichodesma glabrescens* Gürke: 389 (1901). Type: Tanzania, Kinga-Berge, Ussangu, Goetze 1267 (BR, E, iso.—K, photo.?).

**T. ringoetii** De Wild.: 100 (1914). Type: Zaire, Katanga, Nieuwdorp, Ringoet 6 (BR, holo.).

Perennial herb with 1 to several annual stems from a woody rootstock, up to 0.5 m tall. Stems ± glabrous, with scattered setae; young stems fleshy, pinkish. Leaves sessile, bluish green; blade broadly ovate to narrowly ovate, 30–50(–75) × 12–16(–32) mm, base cuneate to rounded, apex acute or obtuse, upper surface clothed with short,
stiff setae; setae all pointing ± in same direction, multicellular base discoid, 3–5-layered; lower surface with scattered setae on midrib and veins only. Inflorescences terminal, cymose panicles, cymules scorpionoid; pedicels up to 30 mm long, drooping. Calyx brownish purple; lobes 13–15 × 5–7 mm in flower, up to 30 × 18 mm in fruit. Corolla white with brown gibbosities at sinuses between lobes, 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 prominent 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, Zaire, Zambia, Malawi, Zimbabwe and Mozambique. Habitat: grassland, woodland, open mixed bushveld, hill slopes, disturbed areas, road sides, 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).

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).


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

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

*T. tinctorum* 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* 4 ± 14 × 8 in flower, ± 22 × 15 mm in fruit. *Corolla* deep blue, pale lavender to white with raised amber-brown gibbosities at sinusae of petal lobes; tube campanulate, lobes reflexed, acipes 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. africannum*;
3. *T. angustifolium* subsp. *angustifolium*;
4. *T. angustifolium* subsp. *argentum*;
5. *T. physaloides* subsp. *hockii*.

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

*Balawk* 1499 (1) NU, PRE. *Balkwell* & *Cadman* 3501 (4) E, PRE. *Balsinhas* 3014 (3a) K, PRE. *Balsinhas* & *Kersberg* 2006 (2) PRE, *Barnard* *SAM6092* (2) SAM. *Barnett* 132 (1) K, PRE. *Bengis* 463 (2) Bolus 641 (2) BM, K, 5713 (3a) K, 6443 (3a) BOL, PRE; 9706 (4) BOL, 10390 (2) BOL, Bond 842 (2) NBG. *Booth & Mason* 2541 (3a) PRE. *Boss* 18, ABO, TRV25550 (3a) PRE; TRV36168 (2) PRE. *Botha & Ubbink* 1733 (3a) PRE. *Boucher* 5147 (2) NBG. *Bradfield* 583 (2) K, PRE. *Bremekamp* TRV27519 (1) PRE. *Breuer* PRE59361, TRV17580 (1) PRE; PRE59405, TRV20582 (3b) PRE. *Brown* & *Kellogg* 277 (3b) WIND. *Bryant* J118 (2) PRE; 8948 (2) K. *Buchanam* sub Wood 7032 (4) PRE. *Buttendam* 626 (4) K, PRE. *Burchell* 1264 (2) K, PRE. *Burger* & *Louw* 297 (2) NBG, PRE. *Burgoyne* 498 (4) PRU. *Burke* 60, 313 (3a) K, PRE; 13749 (4) PRE. *Burt* *Dover* 2051 (4) PRE; 7048 (3a) K; 11009, 11278, 14493 (3a) NBG.

*Cattel* 314 (2) NBG. *Chennells* 151 (3a) BOL, PRE. *Clarke* 2257 (1) PRE; 1318 (4) PRE. *Codell* 627 (4) PRE; 2084, 6645 (3a) K, PRE. *Cole* 1388 (3a) K, PRE. *Comins* 663 (2) K, PRE. *Compton* 2447, 11530, 20616 (2) NBG; 27100 (4) K, PRE; 28934 (1) NBG. *Craven* 14, 184, 216, 1536, 1936, 3136 (2) WIND. *Crook* M37, 737 (4) PRE. *Crosby* 963 (2) PRE. *Cross* 228 (4) PRE.

*Davidse* 6285 (2) PRE. *Davies*, Thompson & Miller 48, 104 (2) PRE. *Dew* & *Krauf* 1231 (4) PRE. *De Lange* UNIN6718 (4) PRE. *UNIN. *De Sousa* 359 (4) PRE. *De Winter* 419 (5) BM, K, PRE; 2473 (3a) K, PRE. *Wind* & *Gües* 6158 (2) K, PRE. *Wind* & *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. *Driege* s.n. (2) K. *Driey* 52 (2) PRE. *Du Plessis* 814, 1046 (4) PRE, FRU; 3100 (4) K, PRE.

*Edwards* PRE40742 (4) PRE. *Elan-Puttick* 292 (4) PRE. *Exterhasson* 2721 (2) NBG, PRE; 4488 (2) BOL. *Evrand* 9034, 9243 (2) PRE.

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

*Galpin* 502M, 503M (3a) PRE; *Galpin* 594M, 6994 (4) PRE; 9223 (1) PRE; 9288 (4) K, PRE; 11380 (1) K, PRE; 13700 (3a) K, PRE; 14111 (2) BOL, K, PRE; 1566 (5) E. *Galpin* s.n. (4) K. *Galpin* & *Pearson* 1561 (2) BOL. *Kapf* 7506 (2) K, PRE. *Kapf* & *Mading* 3086 (4) PRE; 4575, 5377, 5431 (2) PRE. *Gersner* 3435 (4) NH, 4101 (3a) NH; 5119 (4) K. *Kreb* 5153 (3a) PRE; 6616 (1) PRE. *Gibbs*...
REFERENCES


BROWN, R. 1810. Staatssammlung, Muenchen.


MARTINS. E.S. 1893. Sobre a ocorrência de Trichodesma ambacense subsp. hockii em Angola. Garcia de Orta (Serie de Botanica) 11: 2-5.


SOLLINGER. Vienna.


Engler. Leipzig.


Gleditsch. Leipzig.


University Press. Cambridge.

Hilger. H.H.

Robertson.

Nowicke. J.W.

Mason. J.

Wilson. H.

Werne. H.

North. London.

Mason. J.

OUniversity Press. Cambridge.

N. Bulgaria.


SOLLINGER. Vienna.


Engler. Leipzig.


Gleditsch. Leipzig.


Robertson.

Nowicke. J.W.

Mason. J.

Wilson. H.


