



A taxonomic evaluation of the *Thesium confine* species complex (Santalaceae)



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Background: *Thesium* L. is the largest genus in the family Santalaceae (sandalwood family). The last taxonomic revision of the southern African species dates back to 1925. An urgent revision of the genus is required as indicated in a recent national biosystematics research strategy for South Africa.

Objectives: To revise the *Thesium confine* species complex (*Thesium durum*, *T. confine* and *Thesium spartioides*) and to update the typification, nomenclature, descriptions and distribution ranges.

Method: Morphological characters were studied using own field collections as well as herbarium specimens from K, NU, PRE and PRU and images on Global Plants (JSTOR). Distribution ranges of the studied species were updated.

Results: An examination of morphological characters revealed great similarity between *T. spartioides* and *T. confine*. Both species have an herbaceous habit, decumbent growth form, terminal (or less frequently axillary) inflorescences and a sympatric northern distribution in South Africa. *Thesium durum* differs from *T. spartioides* and *T. confine* in having a shrubby habit, erect growth form and axillary inflorescences and occurs in the southern part of South Africa.

Conclusion: *Thesium spartioides* is synonymised under *T. confine*, and *T. durum* is retained as a separate species.

Introduction

Thesium L. is the largest member of the family Santalaceae (sensu APG IV 2016 and Thesiaceae sensu Nickrent et al. 2010; sandalwood family), tribe Thesieae (Germishuizen 2000; Jordaan & Burgoyne 2000), and currently includes 305 'accepted' species concepts (The Plant List 2017). The genus is distributed across temperate and tropical regions of both hemispheres but its centre of diversity is in southern Africa. It is a genus of hemiparasitic shrubs or subshrubs with reduced or scale-like leaves, and nut-like fruits (Forest & Manning 2013; Leistner 2000; Nickrent & García 2015). The southern African species are currently divided among four sections (according to Hill 1925): (1) Sect. *Imberbia* A.W.Hill, (2) Sect. *Barbatae* A.W.Hill, (3) Sect. *Penicillatae* A.W.Hill and (4) Sect. *Annulatae* A.W.Hill or two subgenera (according to Hendrych 1972): (1) Subgen. *Thesium* and (2) Subgen. *Frisea* (Rchb. ex Endl.) Peterm. Hill's study focussed only on the southern African species. As the type of the genus (*Thesium alpinum* L.) is of Eurasian origin (included in De Candolle's Sect. *Euthesium* [= *Thesium*]) (De Candolle 1857; Hill 1915; Moore, Verboom & Forest 2010), Hill excluded this section from his classification system and created Sect. *Imberbia* to accommodate the African species that initially belonged to the type section.

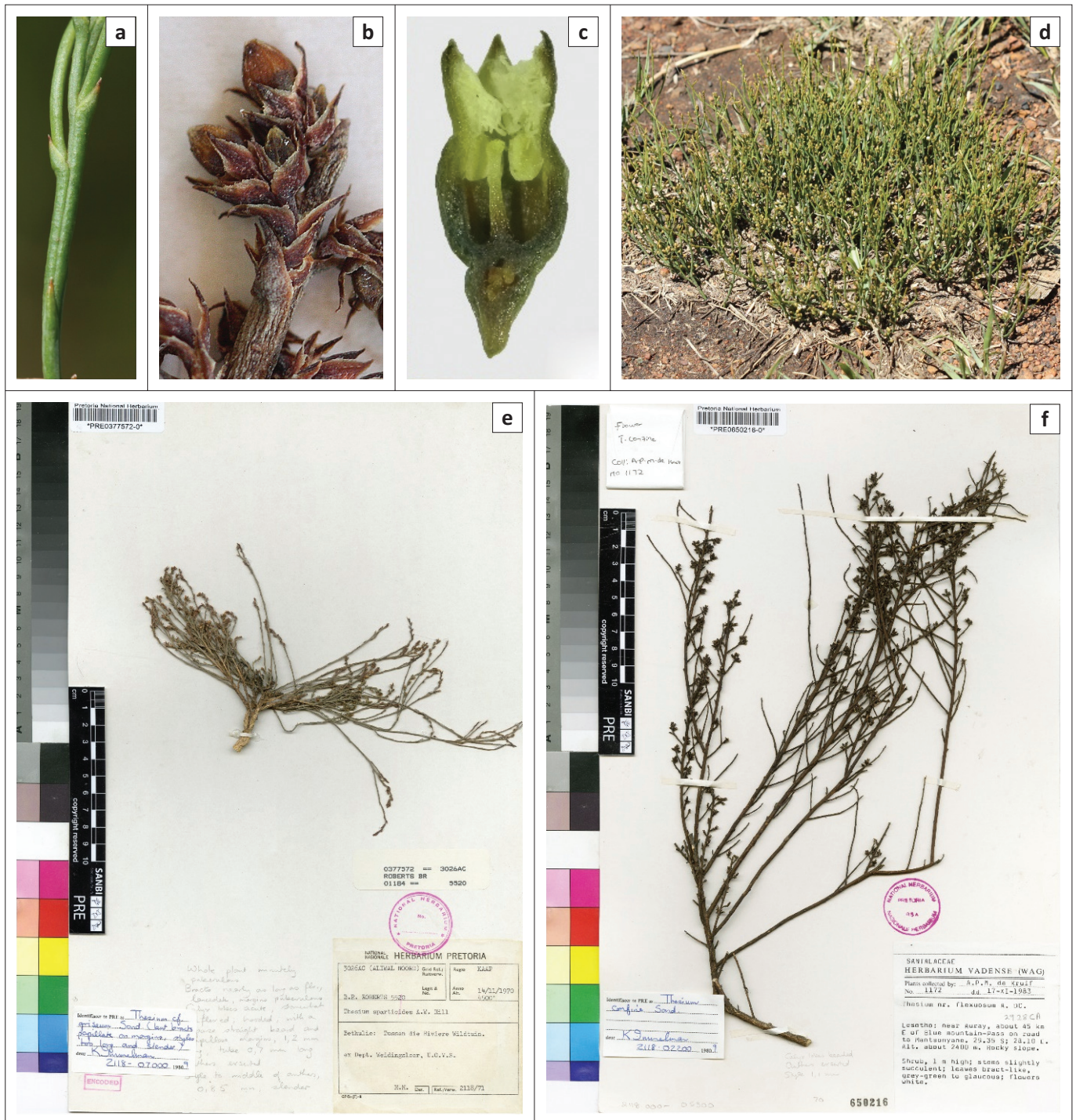
Sect. *Barbatae* is characterised by perianth segments with a dense apical beard (Figure 1c) and anthers attached to the segments or lobes by hairs. *Thesium confine* Sond., *T. durum* Hilliard & B.L.Burt and *T. spartioides* A.W.Hill (hereafter referred to as *T. confine* species complex) form part of the section. These three species occur in the summer rainfall region in South Africa and share a unique combination of morphological characters, which include monotelic, spike-like inflorescences, scale-like leaves, anthers inserted in the tube, perennial habit and placental column twisted (Figure 1), and are often misidentified in the herbarium.

The most recent taxonomic revision for the southern African species dates back to 1925 (Hill 1925) and included only *T. confine* (Sonder 1857) and *T. spartioides* (Hill 1915) as *T. durum* (Hilliard & Burt 1983) was only described later. *Thesium confine* was distinguished from the Cape species, *Thesium capituliflorum* Sond. (indicated by 'proximum'), mainly by having scale-like leaves and 4–6 flowers in spike-like inflorescences, while the latter species has leaves at the bottom and scales

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Source: Photos courtesy of M.M. Le Roux (a–d) and K.S. Mashego (e–f)

FIGURE 1: Morphological characters of *Thesium confine* (a, d, e) and *T. durum* (b, c, f) showing (a) the scale-like leaves found in both species; (b) involucral bracts that are invariably present in *T. durum*; (c) longitudinal section of a flower showing the dense hairs on the perianth lobes, stigma opposite the anthers and the twisted placental column; the habit of (d) *T. confine* and typical herbarium specimens of (e) *T. confine* and (f) *T. durum*.

towards the top, and 3–4 flowers in capitellate inflorescences (Sonder 1857). A single collection of *T. confine* was cited by Sonder (1857) in the protologue. When Hill (1915) described *T. spartioides*, he distinguished it from *T. confine* based on the slender, rush-like stems, shorter inflorescences and longer styles (stout stems, longer inflorescences and shorter styles in *T. spartioides*). Hill (1915) cited only a single collection in the protologue of *T. spartioides*. In Hill's (1925) revision, *T. confine* and *T. spartioides* were distinguished from one

another, respectively, in the key based on slender versus stout stems, ascending versus flexuous or prostrate habit and brown versus grey colour in dried plants. The measurements for the styles given in the descriptions are the same for both species (1 mm in length), providing conflicting information in the key. Three collections were listed for *T. confine* and a single collection for *T. spartioides*. In the protologue of *T. durum*, Hilliard and Burt (1983) distinguished between *T. durum* and *Thesium flexuosum* A.DC. on the basis of dense, lateral

spike-like inflorescences in *T. durum* and elongate spikes in *T. flexuosum* and listed two collections. According to the limited number of specimens given in all of the treatments until 1983, these species are allopatric in their distribution. The latest checklist of *Thesium* (Winter 2006), however, indicates that *T. confine* occurs in the Eastern Cape province and Lesotho, overlapping with *T. spartioides*, which occurs in the Eastern Cape, Free State, Gauteng, Mpumalanga and North West provinces and Lesotho. *Thesium durum* is partially sympatric with *T. spartioides*, occurring in the Free State and KwaZulu-Natal provinces and Lesotho. Although only limited material was available to the authors, they realised that these species should be formally recognised. Today, more specimens are available displaying a larger range of variation, which is not reflected in the current literature. This has led to some confusion and misidentifications in the herbarium, and as a result, species delimitations need to be re-evaluated. An urgent revision of the genus is required, indicated in *A Biosystematics Research Strategy for Plant Taxonomic Research in South Africa* (Victor, Smith & Van Wyk 2015). The aim of this research is to revise the *T. confine* species complex, contributing towards a comprehensive revision, and provide an update of the nomenclature, typification, descriptions, distribution ranges and conservation statuses.

Research method and materials

Herbarium specimens from NU, PRE and PRU, digitised specimens from Global Plants (JSTOR 2017) and images photographed in K were studied (acronyms according to Index Herbariorum; Thiers 2011), including the type specimens. Specimens were divided into three operational taxonomic units (OTUs) based on their morphological characters (habit and growth form, stem diameter and inflorescence structure) and distribution ranges. Three specimens from each OTU were selected for measurements of the vegetative and reproductive morphology. Flowers were placed in boiling water for 2 minutes and dissected under a Zeiss Discovery V8 stereo microscope. Measurements were taken and recorded using the Zeiss stereo microscope and camera and Zeiss ZEN software (Carl Zeiss Microscopy GmbH).

Fieldwork was conducted in October 2016 and 2017 in Mpumalanga province, South Africa, to observe the plants in their natural environment. Specimens were collected and deposited in PRE. Distribution and habitat information were gathered from herbarium specimens and during the field trip.

Results and discussion

All three species are perennials with scale-like leaves and monotelic, spike-like inflorescences. Single flowers within the inflorescence are sometimes replaced by 2- or 3-flowered cymes.

Thesium confine and *T. spartioides* are both herbaceous, with thin, wiry, decumbent stems up to 3 mm diam. and greyish green in colour (Figure 1d and e). *Thesium durum* is shrubby, with relatively thick and erect stems (3 mm – 6 mm diam.)

that are dark brown in colour (Figure 1). The inflorescences are mostly terminal, but may infrequently also be axillary in *T. confine* and *T. spartioides* and are invariably axillary in *T. durum*. In *T. confine* and *T. spartioides*, the number of flowers ranges from five to eight (rarely nine) per inflorescence and involucre bracts are usually absent, while in *T. durum* the number of flowers per inflorescence ranges from one to five (rarely six) and involucre bracts are invariably present. Protologue descriptions were compared to the type and additional specimens in the listed herbaria and the variation observed in *T. confine* and *T. spartioides* are overlapping. No characters could be found to separate the two species from one another as was done by Hill (1915, 1925). Hill studied four specimens, but here 22 specimens were available which revealed more variation than was previously thought to exist. In addition to their similar morphology, *T. confine* and *T. spartioides* are sympatric, occurring in the northern parts of South Africa (in the Mpumalanga, Gauteng, North West, Free State and Eastern Cape provinces; Figure 2). We therefore propose to subsume *T. spartioides* in *T. confine*. *Thesium durum* has a more southerly distribution, occurring from Bethlehem to Cradock (Free State, Northern Cape, Eastern Cape and KwaZulu-Natal provinces and Lesotho). A summary of the morphological characters studied is provided in Table 1.

Taxonomic treatment

1. *Thesium confine* Sond. in *Flora* 40: 363 (1857); DC., *Prodr.* 14: 665 (1857); A.W.Hill in *Fl. Cap.* 5(2): 176 (1925). Type: SOUTH AFRICA, Free State: 'Trans-Garipina, Nieuwejaarspruit, zwischen Garip und Calendonrivier, am Fuss der Witbergen' [Nieuwejaarspruit, between Gariep River and Calendon River, at the foot of Witberg], October, *Zeyher* 114 (S, holo. – digital image!; K, S – digital image!, iso.).

Thesium spartioides A.W.Hill, in *Bull. Misc. Inform. Kew* 1915 (1): 41 (1915); Hill in *Fl. Cap.* 5(2): 176 (1925), *syn. nov.* Type: SOUTH AFRICA, Mpumalanga: 'in collibus pr. Brug Spruit' (on the hills near Brug Spruit), 19 November 1893, *Schlechter*

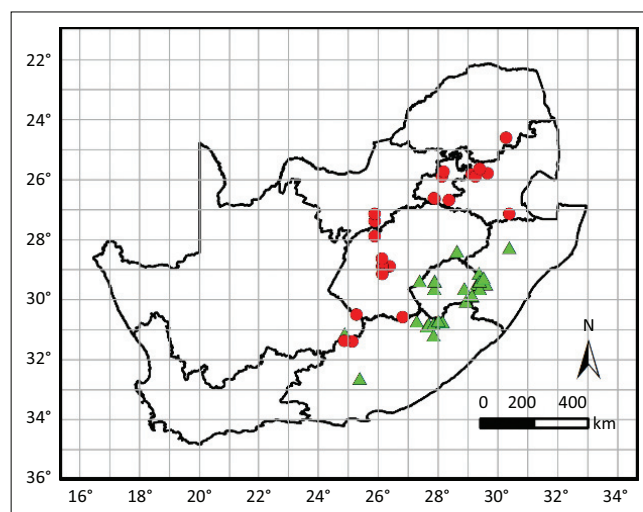


FIGURE 2: Distribution map *Thesium confine* (circles) and *Thesium durum* (triangles).

TABLE 1: Morphological characters studied for *Thesium confine*, *Thesium durum* and *Thesium spartioides*.

Character	<i>Thesium confine</i>	<i>Thesium durum</i>	<i>Thesium spartioides</i>
Habit	Herbaceous perennial	Shrub	Herbaceous perennial
Stem colour when dry	Grey	Dark brown	Greenish to grey
Stem diam.	1 mm – 3 mm	3 mm – 6 mm	1 mm – 3 mm
Growth form	Decumbent	Erect	Decumbent
Leaves	Scales	Scales	Scales
Inflorescence position	Terminal and rarely axillary	Axillary	Terminal and rarely axillary
Inflorescence type	Spike-like (single flowers sometimes replaced by 2- to 3-flowered cymes)	Spike-like (single flowers sometimes replaced by 2- to 3-flowered cymes)	Spike-like (single flowers sometimes replaced by 2- to 3-flowered cymes)
No. of flowers per inflorescence	5–8(9)	1–5(6)	5–8(9)
Involucral bracts	Usually absent	Present	Usually absent

3754 (K, holo. – digital image!; BOL – digital image!, HBG – digital image!, NBG – digital image!; PRE [four sheets]!, S [two sheets] – digital image!, iso.).

Description: Slender perennial with slightly woody rootstock and decumbent habit, branching from rootstock, 70 mm – 280 mm high; stems wiry, 1 mm – 3 mm diam. *Leaves* scale-like, closely adpressed to stem, imbricate on young twigs, lanceolate, acuminate, 1.2 mm – 3.3 mm × 0.2 mm – 0.6 mm, margins ciliate. *Inflorescences* terminal (rarely axillary), monotelic, of 5- to 8(9)-flowered spike-like cymes (with single flowers sometimes replaced by 3-flowered monochasia), peduncles 5 mm – 38 mm long; involucral bracts usually absent; bracts ovate, acuminate, 1.4 mm – 1.5 mm × 1.0 mm – 1.1 mm, adpressed to flower; bracteoles 2, lanceolate, acute, 1.4 mm – 1.7 mm × 1.0 mm – 1.2 mm. *Flowers* white, tubular, subsessile, perianth tube 2.0 mm – 2.4 mm long, lobes ± 1 mm long, densely bearded with white hairs. *Stamens* inserted at base of the perianth tube; filaments 0.1 mm – 0.2 mm long, obscured by anthers; anthers 0.4 mm – 0.5 mm long. *Style and stigma* 0.5 mm – 0.7 mm long, stigma opposite middle or top of anthers. *Placental column* twisted. *Fruit* subglobose, brown, with 10 longitudinal ribbed veins, reticulate between main veins, 2 mm – 3 mm diam., shortly stiptitae, stipe 0.5 mm – 0.7 mm long. *Flowering time:* August to October and December to January.

Distribution and ecology: *Thesium confine* is endemic to northern and interior South Africa, extending from near Wolmaransstad in North West province and Spitskop in the Steelpoort area of Mpumalanga province southwards through Gauteng and Free State to Middelburg in Eastern Cape province (Figure 2). It grows in grassland in sand, clay or loam.

Diagnostic characters and relationships: *Thesium confine* differs from *T. durum* in its herbaceous versus woody habit, slender, decumbent stems up to 3 mm diam. versus thicker, erect stems (3 mm – 6 mm diam.), inflorescences terminal and sometimes axillary versus axillary only, and in usually lacking involucral bracts versus invariably with involucral bracts.

Conservation status: *Thesium confine* is listed as Least Concern because it is widespread and abundant (Foden & Potter 2005b).

Additional specimens seen: SOUTH AFRICA. MPUMALANGA. – **2430 (Pilgrim's Rest):** ± 2 km from Spitskop turn-off off Steelpoort and Lydenburg road, (–CB), 2 Apr. 1997, *M. Jordaan* 3143 (PRE). **2529 (Witbank):** Doornkop 273 JS, vlei wes van Eerstekamp [marsh west of Eerstekamp], (–CB), 29 Oct. 1968, *C.J. du Plessis* 883 (PRE, PRU); El Shaddai, Zeekoeiwater plot 152, Emalahleni, next to the Olifants River, (–CD), 9 Oct. 2016, *N. Visser & M. le Roux* 195 (PRE); next to the road on the R104, 18 km east of Middelburg, (–DC), 26 Oct. 2016, *N. Visser & M. le Roux* 208 (PRE). **2730 (Vryheid):** north of Dirkiesdorp, south-east of main road, (–AB), 13 Dec. 1995, *K. Balkwill* 9398 (PRE).

GAUTENG. – **2528 (Pretoria):** Pretoria, (–CA), 15 Oct. 1963, *H.U. Scheepans & J.C. Stauffer* 5300 (K); Pretoria, norden-Eingang Irene, zwischen Bahn und Wellington-Strasse [northern entrance in Irene, between Bahn and Wellington streets], (–CC), 15 Oct. 1963, *H.U. Stauffer* 5300 (PRE). **2627 (Potchefstroom):** Leeuwkuil Research Station, (–DB), 17 Oct. 1939, *J.P.H. Acocks* 16200 (PRE); Vereeniging, (–DB), 1 Nov. 1911, *R. Leendertz* 3940 (PRE). **2628 (Johannesburg):** Modderfontein, (–CB), 1 Dec. 1943, *A.P.D. McClean* 52808 (PRE).

NORTH WEST. – **2725 (Bloemhof):** Leeuwfontein, 10 km wes van Wolmaransstad plaas van J.J. van Wyk op kalkbanken [10 km west of Wolmaransstad, farm of J.J. van Wyk on kalk bank], (–BB), 25 Mar. 1978, *A.E. van Wyk* 2240 (PRE, PRU); Makwassie, op pad na Wolmaransstad by Leeuwfontein uitdraaipad [Makwassie, on the road to Wolmaransstad at Leeuwfontein turn-off], (–BD), 28 Sep. 1974, *A.E. van Wyk* 570 (PRE).

FREE STATE. – **2725 (Bloemhof):** 5 mi [8.1 km] north-east of Hoopstad, (–DD), 21 Feb. 1946, *J.P.H. Acocks* 12486 (PRE). **2826 (Boshoff):** Boshoff, Modder River, Paardeberg, (–CA), 20 Dec. 1937, *J.P.H. Acocks* 8544 (PRE); Inhoek Krugerdriftdam Nature Reserve, (–CC), 6 Nov. 1974, *D.B. Muller* 1485 (PRE); Glen Agricultural College, (–CD), 21 Jan. 1900, *J.A. van der Berg* 3950 (PRE). **2926 (Bloemfontein):** Bloemfontein, (–AA), Dec., *unknown collector* 1906 (K); Townlands, (–AA), 18 Mar. 1975, *E.R. Anderson* 26 (PRE). **3025 (Colesburg):** Bethulie, Tussen die Riviere Wildtuin, (–AD), 14 Nov. 1970, *B.R. Roberts* 5520 (PRE).

EASTERN CAPE. – **3124 (Hanover):** 3 mi [4.8 km] north-west of Middleburg, (–BD), 10 Mar. 1955, *J.P.H. Acocks* 17970 (PRE). **3125 (Steensburg):** Middleburg; Grootfontein above camp 6, (–AC), 10 Mar. 1955, *J.P.H. Acocks* 17971 (PRE).

2. *Thesium durum* Hillard & B.L.Burt in Notes Roy. Bot. Gard. Edinburgh 41(2): 311 (1983). Type: SOUTH AFRICA, **Eastern Cape:** Fetcani Pass, 15 Oct. 1980, *Hilliard & Burt* 13136 (E – digital image!, holo.; K – digital image!, NBG!, NU!, PRE!, S – digital image!, iso.).

Description: Erect shrub branching above, root structure unknown, 50 mm – 360 mm high; stems relatively thick, 3 mm – 6 mm diam. *Leaves* scale-like, closely adpressed to stem, imbricate on young twigs, lanceolate, acuminate, 1.5 mm – 2.3 mm × 0.2 mm – 0.6 mm, ciliate margins. *Inflorescences* axillary, monotelic, of 1- to 4-flowered spike-like cymes (with single flowers sometimes replaced by 3-flowered monochasia), peduncles 6 mm – 85 mm long; involucre bracts present; bracts ovate, acuminate, 1.4 mm – 1.5 mm × 1.2 mm – 1.6 mm, adpressed to flower; bracteoles 2, lanceolate, slightly narrower than bract, acute, 1.4 mm – 1.5 mm × 0.9 mm – 1.2 mm. *Flowers* white, tubular, subsessile, perianth tube 2.0 mm – 2.5 mm long, lobes ± 1 mm long, densely bearded with white hairs. *Stamens* inserted at base of perianth tube; filaments 0.1 mm – 0.2 mm, obscured by anthers; anthers 0.3 mm – 0.6 mm long. *Style and stigma* 0.3 mm – 0.5 mm long, stigma almost reaching to top of anthers. *Placental column* twisted. *Fruit* ellipsoid, brown, with 10 longitudinal ribbed veins, reticulate between main veins, 2.0 mm – 3.3 mm × 2.4 mm – 3.0 mm, stipe 0.3 mm – 0.5 mm. *Flowering time:* August to October.

Distribution and ecology: *Thesium durum* occurs in eastern South Africa and Lesotho, from Bethlehem in Free State province along the KwaZulu-Natal Drakensberg to Cradock in Eastern Cape province and Hanover in Northern Cape province (Figure 2). It grows on mountainous slopes and rocky outcrops in grasslands, in loam.

Diagnostic characters and relationships: *Thesium durum* differs from *T. confine* in its erect habit with thicker, woody branches and stems 3 mm – 6 mm diam., and axillary inflorescences with involucre bracts.

Conservation status: *Thesium durum* is a Least Concern species because it is widespread and abundant (Foden & Potter 2005a).

Additional specimens seen: SOUTH AFRICA. FREE STATE. – **2828 (Bethlehem):** Bethlehem, Golden Gate National Park, Generaalskop, (–BC), 21 Jan. 1965, *B.R. Roberts* 3432 (PRE).

KWAZULU-NATAL. – **2830 (Dundee):** Drakensberg, Cathkin Peak, (–AB), 1 Jul. 1950, *E.E. Esterhuysen* 17354 (PRE). **2929 (Underburg):** Mpendhle, path from Loteni Nature Reserve to Redi on ridge, (–AD), 26 Dec. 1982, *O.M. Hilliard* 16104 (PRE, K); locality unknown, (–AD), 1 Oct. 1967, *F.B. Wright* 220 (NU); Mpendhle, Mulangane Ridge, above Carter's Nek, (–BC), 13 Mar. 1983, *O.M. Hilliard* 18372 (PRE); Underberg, upper tributaries south of Mkimazi River, (–CB), 30 Nov. 1982, *O.M. Hilliard & B.L. Burt* 15715 (K).

EASTERN CAPE. – **3027 (Lady Grey):** Verge of road up Joubert's Pass, ± 8 km from Lady Grey, (–CB), 25 Feb. 2007, *C.L. Bredenkamp* 26 (PRE); about 15 km east of Rhodes: Mavis Bank Farm, on Kloppershoek turn-off, (–DB), 9 Dec. 1999, *M. Koekemoer* 1559 (PRE); north-east of Rhodes,

Kloppershoekspuit Valley, Mavis Bank Farm, mountain on western side of valley from house, (–DB), 9 Dec. 1999, *L. Smook* 10311 (PRE); Barkly East, 6 mi [9.7 km] north-west of Moshesh Ford, (–DC), 14 Nov. 1959, *J.P.H. Acocks* 20165 (PRE); locality unknown, (–DC), 2 Nov. 1983, *O.M. Hilliard* 16360 (NU); west of Rhodes, Maartinshoekspuit Valley, Maartindale Farm, (–DD), 12 Dec. 1999, *L. Smook* 10399 (PRE). **3028 (Matatiele):** About 15 km east of Rhodes: Mavis Bank Farm; on Kloppershoek turn-off, (–CA), 8 Dec. 1999, *M. Koekemoer* 1524 (PRE); Glen Lynden Farm, top of Naude's Nek Pass, (–CA), 20 Oct. 1994, *S.P. Bester* 3013 (PRE); north-east of Rhodes, Kloppershoekspuit Valley, Mavis Bank Farm, at house, (–CA), 7 Dec. 1999, *L. Smook* 10232 (PRE). **3225 (Somerset East):** Cradock, 1.5 mi [2.4 km], south-east of Lexton Springs, (–CB), 3 Jan. 1959, *J.P.H. Acocks* 20123 (PRE).

NORTHERN CAPE. – **3124 (Hanover):** Colesberg, 9 mi [14.5 km] east by south of Naauwpoort, (–BB), 30 Oct. 1953, *J.P.H. Acocks* 17521 (PRE).

LESOTHO. – **2927 (Maseru):** Mafeteng, Ribaning stream, hillside above stream, (–AD), 22 Oct. 1946, *E.E. Esterhuysen* 13207 (PRE); mountain road, *Leucosidea* forest, (–BD), 1 Oct. 1963, *M.O. Schmitz* 2713 (PRE); mountain road, 5 km before Bushman Pass, (–BD), 2 Nov. 1977, *M.O. Schmitz* 8030 (PRE). **2928 (Marakabei):** Near Aurey, 45 km east of Blue Mountain Pass on road to Mantsonyane, (–CA), 17 Nov. 1983, *A.P.M. de Kruif* 1172 (PRE); Orange valley, between Sehlabathebe and Thaba Tseka, (–DB), 29 Oct. 1979, *M.O. Schmitz* 8859 (PRE). **2929 (Underburg):** Locality unknown, (–CC), 20 Nov. 1983, *O.M. Hilliard & B.L. Burt* 16817 (NU); Sehlabathebe National Park, Matsa a Mafikeng, (–CC), 5 Nov. 1976, *A.C. Beverly & F.K. Hoener* 375 (PRE). **3028 (Ramatselis):** Ramatselis gate (4 km), (–BB), 1 Nov. 1979, *M.O. Schmitz* 8830 (PRE); locality unknown, (–CC), 13 Nov. 1983, *O.M. Hilliard* 16621 (NU).

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

The authors contributed equally to this research and also in editing the article. K.S.M. compiled the first manuscript, and both the authors examined the specimens.

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