South African Journal of Botany 138 (2021) 193–208

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

A taxonomic revision of the *Thesium scirpioides* species complex (Subgenus *Frisea*, Santalaceae) near endemic to South Africa

Natasha Lombard[a,b,*], M. Marianne le Roux[a,b], Ben-Erik van Wyk[b]

[a] Foundational Biodiversity Science Division, National Herbarium, South African National Biodiversity Institute, Private Bag X101, Pretoria 0001, South Africa
[b] Department of Botany and Plant Biotechnology, University of Johannesburg, PO Box 524, Auckland Park 2006, South Africa

ARTICLE INFO

Article History:
Received 25 August 2020
Revised 4 December 2020
Accepted 7 December 2020
Available online 12 January 2021

Edited by GV Cron

Keywords:
Hemi-parasite
scale-like leaves
Subgenus *Frisea*
systematics
Thesiaceae

ABSTRACT

Thesium L. is in need of revision and has been identified as a high priority for taxonomic research in South Africa. As part of an ongoing effort to revise the genus, a group of nine morphologically similar taxa from Subgenus *Frisea* is revised, including three taxa classified by the IUCN as data deficient due to taxonomic problems and one species new to science (*T. atratum* N.Lombard & M.M.le Roux). Species of the group, referred to here as the *T. scirpioides* complex, share the following characters: (1) inconspicuous unarmed herbs or suffrutices, (2) scale-like leaves, (3) indeterminate spike-like inflorescences, (4) post-staminal hairs attaching the anthers to the perianth and (5) twisted placental columns. A comprehensive taxonomic revision of the *T. scirpioides* complex is presented, including an identification key, updated nomenclature and typifications, descriptions, diagnostic characters, distribution maps and conservation notes. Seven species are recognised and two varieties newly synonymised.

1. Introduction

Thesium L. is a genus of hemi-parasitic plants in the Santalaceae (The Angiosperm Phylogeny Group, 2016; or Thesiaceae sensu Nickrent et al., 2010). They grow as herbs, subshrubs or shrubs with predominantly linear or scale-like leaves that usually lack petioles, and have dry, nut-like fruits [except for fleshy fruits in species such as *T. canariense* (Stearn) J.C.Manning & F.Forest, *T. subsucculentum* (Kämmer) J.C.Manning & F.Forest, *T. scandens* E.Mey. ex Sond. and *T. radicans* Hochst. ex A.Rich.] that often form elaiosomes (De Candolle, 1857; Hill, 1925; Nickrent and García, 2015; Zhigila et al., 2020). *Thesium* has about 350 species with a predominantly old-world distribution (Nickrent and García, 2015; Lombard et al., 2020). The majority of species are found in southern Africa (± 175 species), followed by ± 90 species in central, east, west and north Africa, ± 70 species in Eurasia, seven species in Madagascar, four species in the Americas and one species in Australia (Lombard et al., 2020). The genus is currently classified into five subgenera [*Hagnothesium* (A.DC.) Zhigila, Verboom & Muasya, *Thesium, Discothesium* (A.DC.) Zhigila, Verboom & Muasya, *Psilothesium* (A.DC.) Zhigila, Verboom & Muasya and *Frisea* (Rchb.) Hendrych] based on molecular phylogenetic data (Zhigila et al., 2020).

The most recent comprehensive taxonomic treatment of South African *Thesium* species was done by Hill (1915, 1925), where he recognized 128 species in four sections (*Annulata* A.W.Hill, *Barbata* A.W. Hill, *Imberbia* A.W.Hill and *Penicillata* A.W.Hill). The taxa studied here are included in both Sections *Barbata* and *Imberbia* (Hill, 1925). However, molecular studies have recently shown that the sections proposed by Hill are artificial (Moore et al., 2010; Garcia et al., 2018; Zhigila et al., 2020). Hill's treatment and identification key of *Thesium* has also become outdated due to amongst others ca. 50 new South African species being described (e.g., Brown, 1932; Brenan, 1979; Zhigila et al., 2019b) and previously unknown infra-specific variation being observed (Visser et al., 2018; Garcia et al., 2018). *Thesium* is therefore a continuing high priority for taxonomic research in South Africa (Victor et al., 2015; Victor, 2020).

As part of a current effort to revise the taxonomy of the genus, taxonomic revisions of some species groups in southern Africa have been published (Visser et al., 2018; Mashego and le Roux, 2018; Zhigila et al., 2019a) and 11 species newly described (Garcia et al., 2018; Visser et al., 2018; Lombard et al., 2019; Zhigila et al., 2019a, 2019b). We continue this work by revising a group of nine morphologically similar taxa that are near endemic to southern Africa (*T. flexuosum* A.DC., *T. junceum* Bernh. var. *junceum, T. junceum* var. *mammosum* A.W.Hill, *T. junceum* var. *plantagineum* A.W.Hill, *T. lisae-mariae* Stauffer, *T. natalense* Sond., *T. paronychioides* Sond., *T. atratum sp. nov.* and *T. scirpioides* A.W.Hill). This taxon group is referred to here as the *T. scirpioides* species complex. Taxa of the *T. scirpioides* complex fall within Subgenus *Frisea* (ca. 103 species), one of the five

* Corresponding author at: Foundational Biodiversity Science Division, National Herbarium, South African National Biodiversity Institute, Private Bag X101, Pretoria 0001, South Africa.
E-mail address: n.lombard@sanbi.org.za (N. Lombard).

https://doi.org/10.1016/j.sajb.2020.12.005
0254-6299/

subgenera recently proposed by Zhigila et al. (2020) in their phylogeny-based classification of *Thesium*. Species of subgenus *Frisea* exhibit a wide range of morphologies and although subgenus *Frisea* is a well-supported monophyletic clade, interspecific relationships are still largely unresolved (Zhigila et al., 2020). Three of the species in the *T. scirpioides* complex (*T. flexuosum, T. lisae-mariae* and *T. paronychioides*) are included in the phylogeny, and while it appears that these species may be paraphyletic, insufficient information is available to prove this conclusion (Zhigila et al., 2020). The clades in which these three species are placed are not well resolved (Zhigila et al., 2020). Furthermore, the nuclear and plastid phylogenies are incongruent in the placement of *T. flexuosum* and *T. paronychioides* (Zhigila et al., 2020). In the nuclear phylogeny these two species group together, although with weak support (Zhigila et al., 2020).

In the absence of complete information on monophyletic groupings, taxonomic studies rely on practical comparisons among morphologically similar species. Plants of the *T. scirpioides* complex are morphologically similar and are characterized by their 1) inconspicuous unarmed herbaceous or suffrutescent habits, 2) scale-like leaves, 3) indeterminate (polytelic) spike-like inflorescences, 4) post-staminal hairs attaching the anthers to the perianth and 5) twisted placental columns (Fig. 1). The complex occurs across Eswatini, Lesotho, southern Mozambique, and the Eastern Cape, Free State, Gauteng, KwaZulu-Natal, Mpumalanga and Western Cape provinces of South Africa. While a few species from tropical Africa and South America (e.g., *T. aphyllum* Mart. ex A.DC., *T. brachyanthum* Baker and *T. vimineum* Robyns & Lawalrée) share some of the characteristic features of species in the *T. scirpioides* complex, they are geographically separated. Three of the nine taxa treated here, *T. junceum* var. *mammosum, T. junceum* var. *plantagineum* and *T. lisae-mariae,* are currently listed as data deficient due to taxonomic problems in the Red List of South African Plants (Raimondo et al., 2009) and require further

Fig. 1. Diagnostic characters of the *Thesium scirpioides* complex: A, B. Indeterminate spike-like inflorescences. C, D. Scale-like leaves. E. Post-staminal hairs present and attaching anthers to the perianth. F. Twisted placental column. G, H. Unarmed habit. Photographs by M.M. le Roux.

Table 1
A comparison of 18 morphological diagnostic characters for the seven species recognised within the *Thesium scirpioides* complex. Rare character states are indicated in brackets and missing data are indicated with a "?".

Character and character states	T. atratum sp. nov.	T. flexuosum	T. junceum	T. lisae-mariae	T. natalense	T. paronychioides	T. scirpioides
Life form (+ suffrutex, ++ perennial herb, +++ annual)	+	+	++	+	++	(++?)/+++	++
Plant height (m)	≤1	≤0.5	≤0.5	≤0.8	≤0.75	≤0.14(0.25)	≤0.35
Habit (+ divergent to spreading, ++ erect, +++ virgate)	++	+/++	+/++/(+++)	+/(++)	++	++	++/+++
Number of stems at ground level	?	(1)2–27	1–21(40)	1(?)	1–3	1	1–17
Branching position (+ lower third, ++ middle third)	+	+	+/++	+	++	+	+
Inflorescence length (mm)	≤125	≤85	≤225	≤180	≤380	≤70	≤160
Number of flowers per inflorescence	(34)47–116	18–73	4–132	22–31	17–89	18–29	7–22
Number of flowers per cm in the middle of the inflorescence	5–17	4–18	2–14	3–7	2–5	4–6	0–2
Bract colour (+ green/brown, ++ dark brown/black)	++	+	+	+	+	+	+
Sterile bracts (+ absent, ++ present)	?	+	+/(++)	+	+	+	+
Bract margins (+ not cartilaginous, ++ cartilaginous)	+	++	++	++	+/(++)	++	+/(++)
Corolla lobe hood length (mm)	0.2–0.3	0.4–1.0	0.2–0.5	±0.3	0.2–0.3	±0.6	0.1–0.3
Corolla lobe indumentum (+ papillate, ++ bearded, +++ verrucose, ++++ glabrous)	+++/++++	+/(+++)	++	+++/++++	++	+	++
Flat disc (+ absent, ++ present)	++	+	+	++	+	+	+
Style (+ sessile to subsessile, ++ short)	+	+/++	+	+	+	+	+
Anthers (+ inserted in tube, ++ half inserted in tube, +++ exerted from tube)	+++	++	+	+++	+	+	+
Fruit length (mm) (without perianth)	3.2–4.2	2–3	2.0–2.8	±3.7	2.2–3.4	3.3–3.4	3.5–5.1
Fruit stipe length (mm)	(1.2)1.5–2.0	0.2–0.4	0.3–0.6	±1.0	0.4–0.9	0.3–0.4	0.6–1.0

taxonomic study. In addition, plants of the *T. scirpioides* complex are often misidentified due to a lack of effective identification keys and poorly curated herbarium collections, as is often the case with plants of the genus.

The aims of this study were therefore to 1) reassess and confirm taxon concepts within the *T. scirpioides* species complex, 2) provide a full taxonomic treatment for each taxon, including information on nomenclature, typification, diagnostic characters, geographical distribution, conservation status and a description, and 3) provide an up-to-date identification key for species of the complex. Six species are recognised in this treatment, including one species new to science (*T. atratum*), and two varieties are reduced into synonymy.

2. Materials and methods

The morphology of about 360 herbarium specimens from BM, GRA, K, NBG (including SAM), NH, NU, PCE and PRE were studied, as well as images of type specimens on JSTOR Global Plants (https://plants.jstor.org). Four of the seven species treated here were also collected, observed and photographed during several field trips conducted throughout South Africa between October 2016 and March 2020. Specimens collected were deposited in PRE. All herbarium acronyms follow Thiers (2019).

Morphological information was taken from five specimens of each taxon where possible. Specimens covering the entire range of variation of each taxon were selected. Data gathered from 18 morphological characters (five vegetative and 13 reproductive characters) were used to define taxon boundaries following a morphological species approach (see Table 1). Floral and fruit measurements were taken with ZEN lite software v. 2.0 (Carl Zeiss Microscopy GmbH, 2011) using a Zeiss 60 N–C, 2/3″, 0.63 × camera mounted on a Zeiss Discovery V8 Stereo microscope. Flowers and floral bracts were also photographed using a Zeiss Axio Zoom V16 microscope with motorised Z-stacking capability and an AxioCam MRc high resolution camera (Agricultural Research center, ARC) to collect some images used in Figs. 1, 3 and 4. Flowers were rehydrated for 10 min in "Windolene" (a cleaning agent) prior to dissecting and photographing.

The geographical distribution of each taxon was determined using specimen locality information and localities found during field trips. Localities were confirmed, and where necessary georeferenced, using QGIS v. 2.18.25 software (QGIS Development Team, 2018). Specimens are cited according to the Leistner and Morris (1976) quarter degree grid reference system. Final distribution maps were produced using ArcMap v. 10.3.1 (ESRI, Inc., 2015). Photographs and figures were edited and compiled using Microsoft Publisher v. 14.0.7181.5 (Microsoft Corporation, 2010) and Adobe Photoshop Elements 11 software (Adobe, 2012). For conservation status assessments, extent of occurrence (EOO) and area of occupancy (AOO) were calculated with GeoCAT software (http://geocat.kew.org/).

3. Results and discussion

Species in the *T. scirpioides* complex are inconspicuous unarmed herbs or suffrutices with scale-like leaves, indeterminate spike-like inflorescences, post-staminal hairs attaching the anthers to the perianth and twisted placental columns (Fig. 1). A combination of five vegetative and 13 reproductive morphological characters was used to distinguish among species of the complex: life form, plant height, habit, number of stems at ground level, branching position, inflorescence length, number of flowers per inflorescence, number of flowers per cm in the middle of each inflorescence, bract colour, presence or absence of sterile bracts, bract margin characteristics, corolla lobe hood length, corolla lobe indumentum, presence or absence of a flat disc, style position, anther position, fruit length and fruit stipe length. These characters are discussed below along with other relevant characters (a summary is provided in Table 1).

3.1. Vegetative characters

3.1.1. Habit

Within the *T. scirpioides* complex *T. junceum, T. natalense* and *T. scirpioides* are perennial herbs, *T. paronychioides* is an annual herb and *T. flexuosum, T. atratum* and *T. lisae-mariae* suffrutices. With the exception of *T. atratum* and *T. paronychioides*, all species have woody rootstocks with vegetative scales at ground level. Unique to the complex, *T. paronychioides* has a slender non-woody rootstock that lacks vegetative scales altogether. The rootstock of *T. atratum* has not yet been observed.

Species of the complex grow more or less erect with subtle variation depending on the local environment. *Thesium junceum* plants can also be divergent or virgate, *T. paronychioides* and *T. lisae-mariae* ascending-erect and *T. scirpioides* erect-virgate. *Thesium flexuosum* has a polymorphic habit ranging from erect to spreading to decumbent. *Thesium lisae-mariae, T. atratum* and *T. natalense* are the tallest species in the complex, growing up to 0.8 m, 1 m and 0.75 m high respectively, while *T. paronychioides* and *T. scirpioides* are the shortest species, growing up to 0.14(0.25) m and 0.35 m high respectively.

The number of stems at ground level and their branching positions are very useful when distinguishing among species of the *T. scirpioides* complex (Fig. 2). *Thesium junceum, T. lisae-mariae, T. paronychioides, T. atratum* and *T. scirpioides* branch from the lower third upwards, but *T. scirpioides* can also be unbranched. *Thesium natalense* usually branches from the middle third upwards. *Thesium paronychioides* is furthermore often characterized by a single stem branching into several stems between about 15–18 mm above ground (Fig. 2H). *Thesium lisae-mariae* (Fig. 2F) seems to share the before mentioned branching pattern with *T. paronychioides*, but this character needs verification in *T. lisae-mariae* as the lower third is only known from one specimen [*Stauffer, Jacot-Guillarmod & Wells 5173* (K)]. *Thesium flexuosum, T. junceum* and *T. scirpioides* usually have numerous stems at ground level [(1)2–27, 1–21(40) and 1–17 stems respectively], while *T. natalense* has 1–3 stems and *T. paronychioides* a single stem. In *T. atratum* the number of stems at ground level have not yet been observed.

3.1.2. Leaves

Species of the *T. scirpioides* complex all have scale-like leaves (i.e. reduced or rudimentary leaves) which are adpressed and decurrent (Fig. 1C,D), although young plants of *T. flexuosum* occasionally have well-developed ascending leaves. The presence of scale-like leaves is not unique to the *T. scirpioides* complex but in combination with the other diagnostic characters, provide a clearly delimited group.

3.2. Reproductive characters

3.2.1. Inflorescences

Although all species in the *T. scirpioides* complex have indeterminate spike-like inflorescences (Fig. 1A,B), several inflorescence characters are diagnostic. *Thesium junceum* is unique within the complex in that its inflorescences often have sections with sterile bracts interspersed between sections with flowers (Fig. 1B). The sterile bracts can be distinguished from the scale-like leaves by their erose (irregularly toothed) and prominently cartilaginous margins versus erose and slightly cartilaginous margins in the scale-like leaves (not particularly clear in the other six species). Inflorescence length, and number of flowers and flower density per inflorescence also differ among species. *Thesium junceum* and *T. natalense* have the longest inflorescences in the complex (up to 225 mm and 380 mm long respectively), while *T. flexuosum* and *T. paronychioides* have the shortest inflorescences (up to 85 mm and 70 mm long respectively). The inflorescences of the remaining species grow up to 125 mm (*T. atratum*), 160 mm (*T. scirpioides*) and 180 mm long (*T. lisae-mariae*). In terms of flower number and density per inflorescence, *T. scirpioides* has by far

Fig. 2. Scans of representative herbarium specimens of all the species in the *Thesium scirpioides* complex to show the differences in habit and branching patterns. A, B. *T. flexuosum*. C. *T. junceum* var. *plantagineum*. D. *T. junceum* var. *junceum*. E. *T. atratum*. F. *T. lisae-mariae*; showing the single stem at ground level. G. *T. natalense*. H. *T. paronychioides*; showing the single stem at ground level, and I. *T. scirpioides*. Images © South African National Biodiversity Institute. Reproduced with the consent of the South African National Biodiversity Institute (A-E, G-I); © The Board of Trustees of the Royal Botanic Gardens, Kew. Reproduced with the consent of the Royal Botanic Gardens, Kew (F).

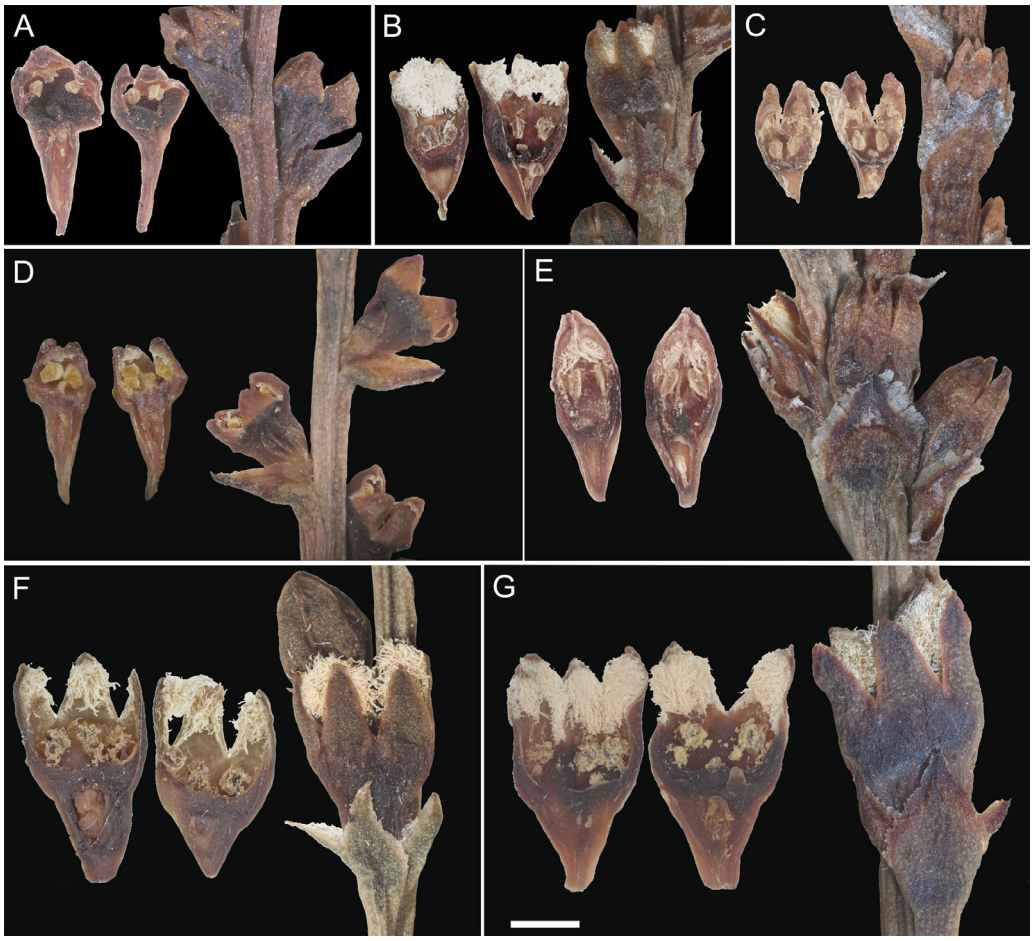

Fig. 3. Longitudinal sections of flowers, showing the indumentum and its distribution on the corolla lobes, length of the style, the stigma position in relation to the anthers and the configuration of the flowers, bracts and bracteoles on the peduncles. A. *Thesium atratum* [*Marloth 10,952* (PRE)]. B. *T. junceum* [*Bayliss 7636* (PRE)]. C. *T. paronychioides* [*Schlechter 2428* (PRE)]. D. *Thesium lisae-mariae* [*Stauffer, Jacot-Guillarmod & Wells 5173* (PRE)] E. *T. flexuosum* [*Esterhuysen 19,473* (PRE)]. F. *T. natalense* [*Acocks 11,841* (PRE)]. G. *T. scirpioides* [*Philips 3224* (PRE)]. Scale bar = 1 mm. Photographs by M.M. le Roux (A–G).

the most sparse inflorescences with 7–22 flowers per inflorescence and only 0–2 flowers per cm in the middle of the inflorescence, followed by *T. paronychioides* (18–29 flowers per inflorescence and 4–6 flowers per cm in the middle of the inflorescence) and *T. lisae-mariae* (22–31 flowers per inflorescence and 3–7 flowers per cm in the middle of the inflorescence). In contrast, *T. junceum* can have the most flowers in an inflorescence (4–132 flowers; 2–14 flowers per cm in the middle of the inflorescence) and *T. flexuosum* the most densely arranged flowers (18–73 flowers per inflorescence; 4–18 flowers per cm in the middle of the inflorescence). *Thesium atratum* also has many-flowered inflorescences [(34)47–116 flowers per inflorescence] with densely arranged flowers [5–17 flowers per cm in the middle of the inflorescence]. *Thesium natalense* has 17–89 flowers per inflorescence and 2–5 flowers per cm in the middle of the inflorescence.

3.2.2. Bracts and bracteoles

All species in this complex have more or less similar ovate to rhomboid bracts and bracteoles (Fig. 3). In *Thesium* species the bracts are predominantly longer than the bracteoles, or occasionally equal in length. The opposite is sometimes true in *T. flexuosum* and *T. junceum* with the bracteoles often being slightly longer than the bracts, but this character varies within species. Differences between species can be found in the bract margins (Fig. 3). *Thesium flexuosum* and *T. paronychioides* have strongly erose and broadly cartilaginous margins. The bracts of *T. junceum* are similar to those of *T. flexuosum* and *T. paronychioides* but not as broadly cartilaginous. *Thesium lisae-mariae* has entire to erose and somewhat cartilaginous bract margins. In *T. natalense* and *T. scirpioides* the bract margins are erose and occasionally only slightly cartilaginous, while *T. atratum* has entire to erose, but never cartilaginous bract margins. Cartilaginous margins

Fig. 4. Protuberance on the corolla lobe between the lobe hairs and the anther attachment in *T. junceum* var. *mammosum* [*Paterson 806* (K, holotype)]. Scale bar = 1 mm. Photograph by N. Lombard.

seem to occur due to the bracts dying back layer by layer, starting early on in development. As a result, bract apices range from acute to acuminate and appear increasingly acuminate over time. *Thesium atratum* can easily be distinguished from all other species in the complex by its prominently dark or black bracts that also dry black (Fig. 5B,C). Other species of the *T. scirpioides* complex have green or brown bracts.

3.2.3. Floral structure

With the exception of *T. atratum* and *T. lisae-mariae*, species of the *T. scirpioides* complex have similar more or less tubular shaped flowers without a flattened disc in the base of the tube. *Thesium atratum* and *T. lisae-mariae* on the other hand have patelliform flowers provided with a distinct flattened disc.

Several important diagnostic characters are found inside the flowers (Fig. 3). In the *T. scirpioides* complex these characters tend to vary less than vegetative characters and are very helpful in separating the species. *Thesium flexuosum* and *T. paronychioides* have similar-looking flowers, as well as *T. natalense* and *T. scirpioides*, and *T. lisae-mariae* and *T. atratum.* The corolla lobe apices of species in the *T. scirpioides* complex are more or less hooded. *Thesium flexuosum* and *T. paronychioides* both have prominent hoods, 0.4–1.0 mm long in the former and ± 0.6 mm long in the latter. *Thesium junceum* has slightly shorter hoods (0.2–0.5 mm long) and *T. lisae-mariae, T. atratum, T. natalense* and *T. scirpioides* have very short hoods (only up to 0.3 mm long).

One of the most important diagnostic characters in this species complex is the nature of the hairs on the internal surface of the corolla lobes (Fig. 3). *Thesium atratum* and *T. lisae-mariae* lack hairs or papilla on the corolla lobe apices and margins. *Thesium flexuosum* and *T. paronychioides* are characterised by their papillate corolla lobe apices and the absence of hairs or papilla on the lobe margins. In contrast, *T. junceum, T. natalense* and *T. scirpioides* all have very densely bearded corolla lobe apices and hairs on the lower lobe margins.

Some plants of *T. junceum* have the seemingly unique, albeit variable, character of a prominent fleshy protuberance on the inner surface of each corolla lobe, between the apical beard and the corresponding anther (see **3. *T. junceum***) (Fig. 4). *Thesium nautimontanum* M.A.García, Nickrent & Mucina is characterised by a similar structure but it is rather warty unlike that of *T. junceum* which is entirely smooth (Hill, 1915; García et al., 2018).

Anthers of species in the *T. scirpioides* complex are usually included entirely in the perianth tube, with the exception of *T. flexuosum* in which the anthers are included halfway in the tube, and *T. atratum* and *T. lisae-mariae* in which the anthers are entirely exserted from the tube.

Species of the complex have sessile or subsessile stigmas (styles ≤ 0.3 mm long) except for *T. flexuosum* in which the style lengths range from absent (stigma sessile) to short (0.6 mm long). Linked to the length of the style is the position of the stigma in relation to the anthers. In species of the *T. scirpioides* complex stigmas never reach beyond the middle of the anthers. In *T. natalense* the stigmas reach to the lower half of the anthers, in *T. junceum, T. paronychioides* and *T. scirpioides* only to the bottom of the anthers, and in *T. flexuosum, T. atratum* and *T. lisae-mariae* varies from below the anthers to the lower half of the anthers.

3.2.4. Fruit

The species treated here all have similar globose-ellipsoid fruit with 10 main longitudinal veins and secondary reticulate venation, clearly visible in dry material. Most of the species have fruit that are smaller than 3.5 × 2.6 mm (excluding the perianth), except for *T. lisae-mariae* (3.7 × 2.8 mm), *T. atratum* (3.2–4.2 × 2.0–2.6 mm) and *T. scirpioides* (3.5–5.1 × 2.4–3.6 mm) which have the largest fruit in the complex. Furthermore, *T. lisae-mariae* and *T. atratum* have distinctively long fruit stipes [± 1 mm and (1.2)1.5–2.0 mm respectively], while the remaining species in the *T. scirpioides* complex all have fruit stipes shorter or equal to 1 mm in length.

4. Key to the species in the *Thesium scirpioides* complex

All species of this species complex have (1) sulcate stems when dry, (2) glabrous stems and leaves (occasionally scabrid in *T. flexuosum*), (3) decurrent and adpressed scale-like leaves, (4) indeterminate (polytelic) spike-like inflorescences, (5) post-staminal hairs present and attaching anthers to perianth, (6) twisted placental columns, and (7) 10-ribbed fruits with reticulate secondary venation visible when dry.

1a. Plants annual (or short-lived perennials); ascending-erect; up to 0.14(0.25) m tall . . . . . **6. *T. paronychioides***

1b. Plants perennial; prostrate to erect; up to 1 m tall (if shorter than 0.14 m, then clearly suffrutescent or erect-virgate):

2a. Corolla lobes glabrous or verrucous; anthers exserted entirely from the tube; flat discs present; fruit stipes at least 1 mm long:

3a. Bracts green or brown; bract margins somewhat cartilaginous; 22–31 flowers per inflorescence; 3–7 flowers per cm in the middle of the inflorescence; fruit stipes ± 1 mm long . . . . . **4. *T. lisae-mariae***

3b. Bracts dark brown or black; bract margins never cartilaginous; (34)47–116 flowers per inflorescence; 5–17 flowers per cm in the middle of the inflorescence; fruit stipes (1.2)1.5–2.0 mm long . . . . . **1. *T. atratum***

2b. Corolla lobes papillate or hairy; anthers inserted entirely or halfway in the tube; flat discs absent; fruit stipes up to 1 mm long:

4a. Suffrutices; erect to spreading(decumbent) (growth form polymorphic); inflorescences up to 85 mm long; corolla lobe apices papillate; apex hoods 0.4–1.0 mm long; anthers inserted halfway in the tube . . . . . **2. *T. flexuosum***

4b. Perennial herbs; invariably erect to divergent to virgate; inflorescences up to 380 mm long; corolla lobes apices densely bearded; apex hoods up to 0.5 mm long; anthers entirely inserted in the tube:

5a. Bract margins broadly cartilaginous; sterile bracts often present; 2–14 flowers per cm in the middle of inflorescences; corolla lobes with long hairs at the apex and on the lower margins; apex hoods 0.2–0.5 mm long . . . . . **3. *T. junceum***

5b. Bract margins scarcely cartilaginous; sterile bracts never present; up to 5 flowers per cm in the middle of inflorescences; corolla lobes with long hairs at the apex and shorter hairs on the lower margins; apex hoods 0.1–0.3 mm long:

6a. Slender herbs; up to 0.75 m tall; 1–3 stems; stems branched from the middle third upwards; 2–5 flowers per cm in the middle of inflorescences; fruits (without perianth) 2.2–3.4 × 1.8–2.6 mm . . . . . **5. *T. natalense***

6b. Rush-like herbs; up to 0.35 m tall; 1–17 stems; stems unbranched or branched from the lower third upwards; 0–2 flowers per cm in the middle of inflorescences; fruits (without perianth) 3.5–5.1 × 2.4–3.6 mm . . . . . **7. *T. scirpioides***

5. Taxonomic treatment

1. *Thesium atratum* N.Lombard & M.M.le Roux **sp. nov.** (Fig. 5)

Type: South Africa, Western Cape, Willowmore (3323): Uniondale, Avontuur (–CA), Nov 1921, *Marloth 10,952* (PRE0375276–0, holo.).

Suffrutex, up to 1 m tall, erect. *Stems* multiple (?) at ground level, branched from the lower third upwards. *Leaves* scale-like, rhombic-ovate, 1–2 × 0.8–1.2 mm long, apices acuminate, margins entire to erose and dying back black but not cartilaginous. *Inflorescences* up to 125 mm long with (34)47–116 flowers, usually with one fertile flower and two bracteoles in each bract, 5–17 flowers per cm in the middle of the inflorescence. *Bracts* ovate, 1.1–2.1 × (0.5)0.8–1.0 mm, apices acuminate to attenuate,

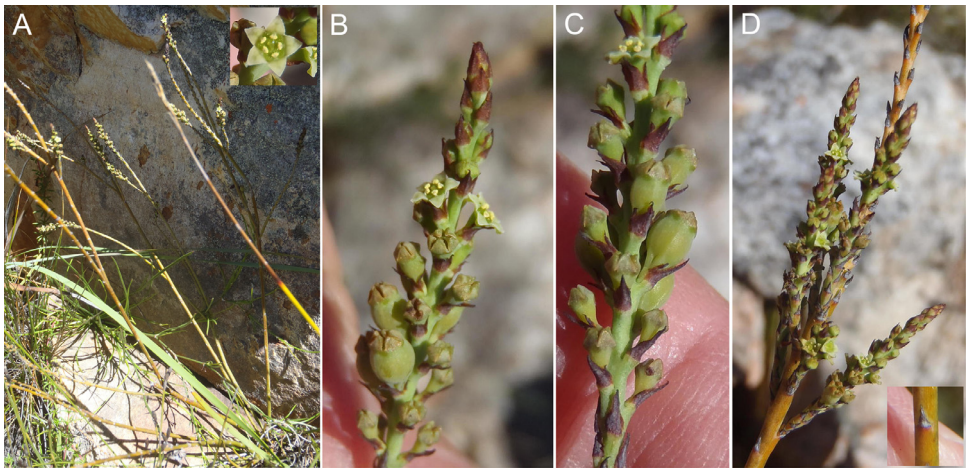

Fig. 5. Morphology of *Thesium atratum*, a new species, characterised by its dark-coloured bracts and bracteoles and compact inflorescences. A. Habit, B–D. inflorescences, A–B. flowers and C. fruit. Photographs by © Nicola van Berkel.

margins entire to erose and dying back black but not cartilaginous, bract apices reaching to middle of flower lobes; bracteoles similar to bracts but smaller. *Flowers* 1.9–3.1 mm long, corolla lobes 0.5–0.7 mm long, glabrous or verrucous at the apex, apices slightly hooded, hoods 0.2–0.3 mm long, flat disc present. *Anthers* entirely exerted from the tube, 0.2–0.3 mm long. *Stigmas* subsessile, below or reaching to the lower half of the anthers. *Fruits* (3.9)4.7–5.0 mm long, stipes (1.2)1.5–2.0 mm long, fruits without perianth 3.2–4.2 × 2.0–2.6 mm.

Distribution and ecology

Thesium atratum is endemic to South Africa. It is currently known from three localities between Baviaanskloof in the Eastern Cape and the Swartberg mountains in the Western Cape (Fig. 6F). It has been collected on sandy rocky soils in *Protea* veld at altitudes between 900 and 1200 m a.s.l. *Thesium atratum* has been collected in flower in November, May and June.

Diagnostic characters

Thesium atratum is morphologically most similar to *T. lisae-mariae* but differs in its many-flowered inflorescences [(34) 47–116 flowers per inflorescence] with flowers arranged close together (5–17 flowers per cm in the middle of the inflorescence), very dark or black bracts with non-cartilaginous margins and longer fruit stipes [(1.2)1.5–2.0 mm long] (Fig. 5) [versus fewer-flowered inflorescences (22–31 flowers per inflorescence) with sparsely arranged flowers (3–7 flowers per cm in the middle of the inflorescence), brown bracts (when dry, likely green when fresh) with cartilaginous margins and shorter fruit stipes (± 1 mm long) in *T. lisae-mariae*].

The specific epithet *atratum* refers to the distinctively dark-coloured bracts and bracteoles.

Conservation status

This newly described species is currently known from three localities with an extent of occurrence (EOO) of 2727 km^2 and area of occupancy (AOO) of 12 km^2. The presence of *T. atratum* within the Kammanassie Nature Reserve was confirmed in 2015 through an iNaturalist record (https://www.inaturalist.org/observations/11153091) and it is likely that several populations persist within the multiple protected areas encompassing this species' distribution range. In the absence of population level data for assessment against Criteria A, C, D and E, we suggest a preliminary conservation status of Endangered (EN) under Criterion B (IUCN Standards and Petitions Subcommittee, 2017).

Additional specimens examined

South Africa. WESTERN CAPE: **3322 (Oudtshoorn)**: Cango Caves, lower southern slopes of Swartberg Mountains, near Swartberg Pass (–AC), 17 Jun 1986, *Vlok 1481* (PRE).

EASTERN CAPE: 3324CA (Steytlerville): Baviaanskloof, Bosrug, on top near road (–CA), 6 May 1995, *Euston-Brown 480* (GRA).

2. *Thesium flexuosum* A.DC. in Esp. Nouv. Thesium: 6 (1857); A.DC. in Prodr. 14: 669 (1857); A.W.Hill in Dyer, Fl. Cap. 5(2): 176 (1925); Goldblatt and J.C.Manning in J. S. African Bot. Suppl. 13: 407 (1984); Bond and J.C.Manning in Strelitzia 9: 641 (2000); J.C.Manning and Goldblatt in Strelitzia 29: 728 (2012); Bredenk. and Germish. in Bredenk., Strelitzia 41(2): 1461 (2019). *Linosyris flexuosa* (A.DC.) Kuntze in Revis. Gen. Pl. 2: 588 (1891). Type: South Africa, Eastern Cape, Port Elizabeth (3325): Uitenhage, Zwartkopsrivier (–CD), Mar without year, *Ecklon & Zeyher 9* (B 10 1067697, lecto. – image!, designated here; G – image!, HBG – image!, K!, MO – image!, W, isolecto.). [*Note: Ecklon & Zeyher 9* (B) is designated as the lectotype of *T. flexuosum*. This specimen is one of the two original syntypes listed by De Candolle (1857). It is chosen as the lectotype because it exhibits an entire plant with the under-ground parts, flowers and fruits, and it also shows the diagnostic characters of the species.]

Suffrutex, up to 0.5 m tall, erect to spreading(decumbent) (growth form polymorphic). *Stems* 2–27 at ground level, branched from the lower third upwards. *Leaves* scale-like, linear- to ovate-triangular(rhomboid), 1.0–2.5 × 0.8–1.8 mm long, apices broadly acute to acuminate, margins entire to erose and slightly cartilaginous. *Inflorescences* up to 85 mm long with 18–73 flowers, usually with one fertile flower and two bracteoles in each bract, 4–18 flowers per cm in the middle of the inflorescence. *Bracts* ovate to broadly ovate and often rhomboid, 1.4–2.3 × 1.0–1.9 mm, apices broadly acute to acuminate, margins strongly erose and broadly cartilaginous, bract apices reaching beyond the flower lobe sinuses; bracteoles similar to bracts but usually slightly longer, rarely somewhat smaller. *Flowers* 1.6–3.3 mm long, corolla lobes 0.7–1.6 mm long, sparsely papillate towards the apex or sometimes almost glabrous, apices hooded, hoods 0.4–1.0 mm long, flat disc absent. *Anthers* inserted halfway in the tube, 0.3–0.6 mm long. *Stigmas* sessile or borne on a short style (0–0.6 mm long), below or reaching to the lower half of the anthers. *Fruits* 2.9–4.5 mm long, stipes 0.2–0.4 mm long, fruits without perianth 2.0–3.0 × 2.0–2.6 mm.

Distribution and ecology

Thesium flexuosum is endemic to South Africa, where it occurs from Bedford and East London in the Eastern Cape westwards to Caledon in the Western Cape (Fig. 6A). This species is found in grasslands and open

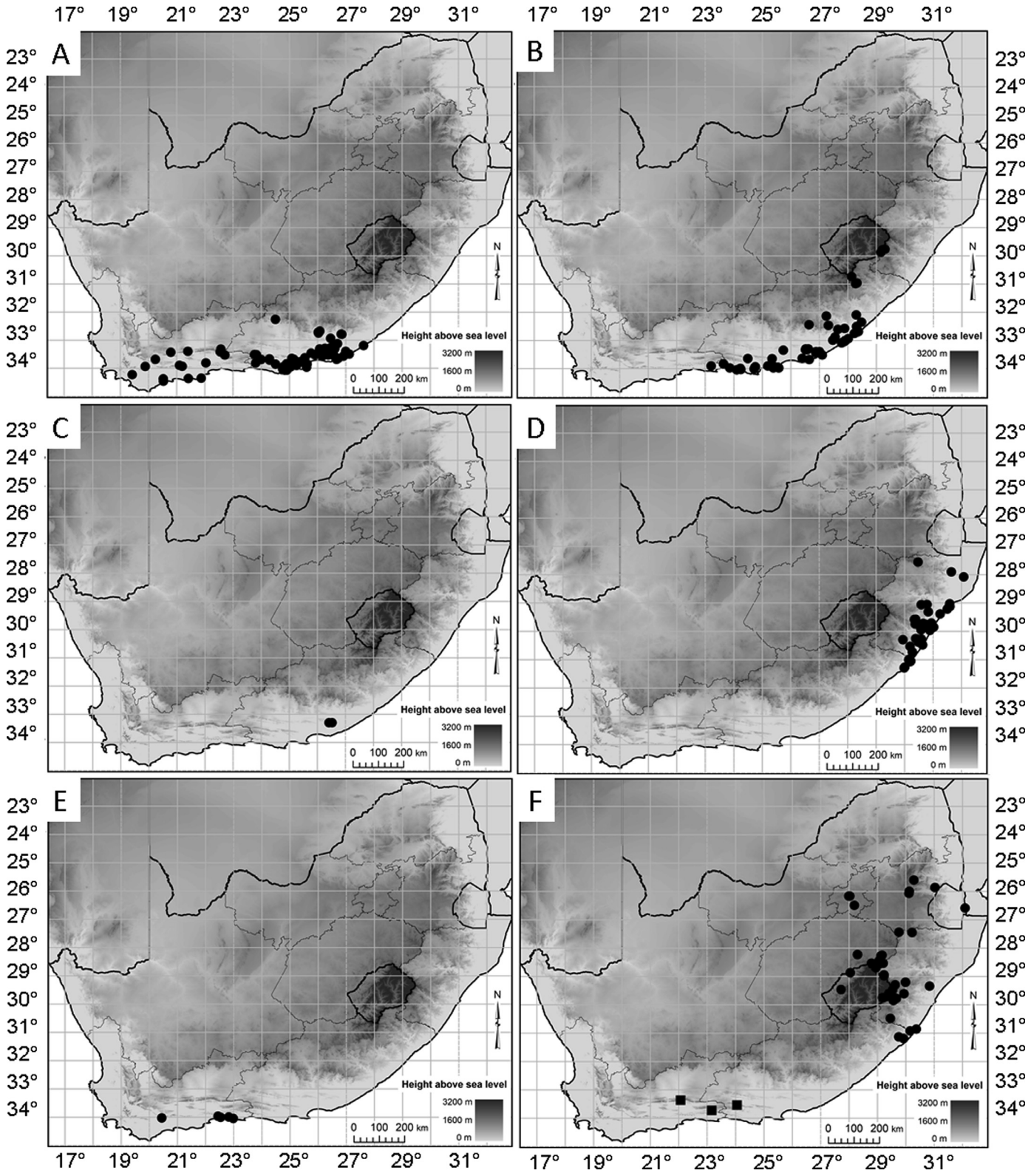

Fig. 6. Known geographical distributions of the seven species in the *Thesium scirpioides* complex. A. *T. flexuosum*. B. *T. junceum*. C. *T. lisae-mariae*. D. *T. natalense*. E. *T. paronychioides*. F. *T. scirpioides* (solid circles) and *T. atratum* (solid squares).

grassy areas in woodlands, dune forest, fynbos, karooid vegetation, renosterveld, sand dunes, shrubland and thicket, as well as on numerous soil types (clay, gravel, loam, rocks and sand) and bedrocks (calcrete, limestone, quartzite, sandstone and shale). It occurs at altitudes between 0 and 975 m a.s.l. Flowering time is usually between August and March, but plants have occasionally been found in flower in May and July.

Diagnostic characters

Thesium flexuosum is similar to *T. paronychioides* but differs in the robust, suffrutescent and spreading to erect habit (polymorphic) (Fig. 2A,B), inflorescences with 18–73 flowers, flowers 1.6–3.3 mm long, corolla lobes 0.7–1.6 mm long, and anthers

inserted halfway in the tube (Fig. 3E) [annual (or possibly short-lived perennial) ascending-erect herb, inflorescences with 18–27 flowers, flowers 2.0–2.3 mm long, corolla lobes ± 0.9 mm long and anthers entirely inserted in the tube in *T. paronychioides*].

Young plants of *T. flexuosum* occasionally have well-developed leaves which do not persist into the adult stage. Furthermore, *T. flexuosum* usually has glabrous stems and leaves but plants with scabrid stems and leaves have been observed.

Conservation status

Thesium flexuosum is locally abundant and therefore appropriately classified as Least Concern (Raimondo et al., 2009; IUCN Standards and Petitions Subcommittee, 2017).

Additional specimens examined

South Africa. WESTERN CAPE: **3319 (Worcester)**: Vrolijkheid Nature Reserve, *koppies aan wesgrens* [hills on W border] (–DD), 20 Jan 1973, *Burgers 86* (PRE). **3320 (Montagu)**: ± 45 km S of Laingsburg on road to Ladismith (–BD), 1 Sep 1999, *Burgoyne 7453* (PRE); 16 mi [25.7 km] NE of Montagu (–CB), 18 Aug 1973, *Wisura s.n.* (NBG). **3321 (Ladismith)**: Ladismith, Sevenweekspoort (–AD), 14 Mar 1981, *Hugo 2580* (NBG, PRE); Little Karoo S of Ladismith, farm Phisantefontein (–CC), 10 Dec 2007, *Burgoyne 11,349* (PRE); Riversdale, Sopieshoogte, N entrance to Garcia's Pass (–CC), 16 Sep 1981, *Fellingham 154* (K, NBG, PRE). **3322 (Oudtshoorn)**: Meiringspoort, E of Oudtshoorn (–BC), 2 Jun 1974, *Goldblatt 1772* (NBG, PRE); Ventershoof, near Klaarstroom farm, slopes above mouth of kloof, behind farm yard (–BC), 17 Sep 1976, *Taylor 9385* (NBG); Outeniqua mountains, N side of Outeniquas near Moeras River (–CC), 6 Dec 1951, *Esterhuysen 19,473* (PRE); ± 18 km E of De Rust (–DA), 15 Aug 2008, *Burgoyne 11,585* (PRE). **3323 (Willowmore)**: Baviaanskloof, 62 km from Willowmore (–DB), 14 Sep 1982, *Immelman 329A* (K). **3419 (Caledon)**: Caledon Division (–AB), *Rogers s.n.* (SAM). **3420 (Bredasdorp)**: De Hoop, Potberg Nature Reserve, 1 km NW of Potberg houses at base of mountain (–BC), 25 Jul 1979, *Burgers 1999* (NBG, PRE); De Hoop, Potberg Nature Reserve, Potberg farm, 3 km from coast along track to coast (–BC), 27 Nov 1978, *Burgers 1536* (NBG). **3421 (Riversdale)**: Still Bay, Panorama Circle above road (–AD), 30 Dec 1978, *Bohnen 4921* (PRE); 9 Jun 1980, *Bohnen 7564* (PRE); flats W of Gouritz River mouth (–BD), 20 Sep 1973, *Thompson 2020* (NBG, PRE).

EASTERN CAPE: **3226 (Fort Beaufort)**: Bedford Catchment West, Brakfontein, slope across road from huts, below the quarry (–CA), 24 Jan 1990, *Hobson 911* (GRA); Bedford Catchment West, W bank of Goba's Drift (–CA), 24 Jan 1990, *Hobson 979* (GRA); Bedford District, Bedford road (–CA), 15 Oct 1966, *Bayliss 3636* (NBG); Kromo mouth, trig beacon at mouth (–CD), 16 Dec 1958, *Acocks 20,104* (K, PRE); Alice, Fort Hare, near main gate (–DD), 12 Sep 1935, *Giffen 414* (PRE); Victoria East, near Keiskama River (–DD), Oct 1928, *Dyer 1658* (GRA). **3323 (Willowmore)**: Baviaanskloof, 62 km from Willowmore (–DB), 14 Sep 1982, *Immelman 329C* (PRE); 3.3 mi [5.3 km] from Joubertina to Avontuur (–DD), 27 Sep 1969, *Marsh 1404* (K, NBG, PRE). **3324 (Steytlerville)**: Cave near Graaff-Reinet (–BC), Dec 1872, *Bolus 813* (K); Humansdorp Division, Kouga hills (–CA), 12 Nov 1941, *Esterhuysen 6663* (K); *6705* (K, PRE); Kouga mountains, Drinkwaterskloof, ridge from Grasskop to Akkerdal, permanent plot #47 (–CB), 8 Nov 2011, *Euston-Brown 1669* (NBG); Kouga, White Ruggens 238, on top of mountain, gentle N facing slope, permanent plot #63 (–CB), 6 Feb 2012, *Euston-Brown 1780* (NBG, PRE); Zitzikama, Welbedacht (–DC), Sep 1909, *Fourcade 489* (GRA); along R331 about 3 air km E of Hankey (–DD), 1 Dec 2007, *Garcia MAG3969* (NBG); Hankey area, about 2.9 km W of Hankey on the R330, next to the road (–DD), 30 Dec 2018, *Visser 379* (PRE); R330 between Humansdorp and Hankey, 8.6 km N of junction with N2 (–DD), 30 Nov 2007, *García & Lopez González MAG3966* (NBG). **3325 (Port Elizabeth)**: Alexandria, Zuurkop, Addo [Elephant] National Park (–BD), 18 Oct 1951, *Archibald 3863* (GRA); Groendal Wilderness Area, (KwaZunga) upper Swartkops Catchment Basin (–CA), 15 Dec 1973, *Scharf 1039* (PRE); Uitenhage Division, Elands River, Groendal Wilderness Reserve, catchment basin (–CA), 15 Mar 1974, *Scharf 1251* (K, PRE); Gamtoos River mouth (–CC), 4 Aug 1982, *Batten 619* (K, NU); *probe* [near] Gamtoos River (–CC), 21 Nov 1894, *Schlechter 6051* (BM, GRA, K, PRE); Uitenhage (–CD), 4 Sep 1912, *Drège 3043* (GRA); Witteklip (–CD), 31 Jul 1932, *Long 651* (K *partly*); 7.5 mi. [12.1 km] N of Port Elizabeth (–DA), 17 Mar 1954, *Acocks 17,617* (K); Suttonvale farm between Centlivres farm and Addo [Elephant National Park] (–DA), 29 Sep 1984, *Schrire 1951* (GRA); Paterson area, about 10.8 km S of Paterson on the N10, next to the road (–DB), 4 Nov 2018, *Visser, le Roux & Simali 374* (PRE); Carbon Black factory, Swartkops (–DC), 21 June 1972, *Jacot-Guillarmod 7355* (GRA); Donkin Reserve (–DC), 23 Sep 1932, *Long 789* (GRA, K, PRE); Redhouse (–DC), Aug 1908, *Paterson 52* (GRA); Uitenhage Division, fields near Zwartkops River (–DC), Oct, *Ecklon 184* (PRE); *Zeyher 184* (K, NBG); *Ecklon & Zeyher (Drège) 3796* (SAM); Zwartkops District (–DC), 24 Dec 1951, *Theron 1174* (K, PRE). **3326 (Grahamstown)**: Alexandria District, Bushmans River Poort, Paynes farm (–AC), 31 Aug 1954, *Archibald 5618* (GRA, PRE); Alicedale (–AC), 6 Oct 1917, *Cruden 76* (GRA); Albany Division, Highlands, Rockdale (–AD), Nov 1939, *Dyer 2217* (PRE); Albany Division, *Strasse im Begleitsaum, Cradock road, ± 8 meilen* [12.9 km] *richtung NW von Grahamstown* [on the road, in the companionway, Cradock road, about 8 mi [12.9 km] northwest of Grahamstown] (–AD), 14 Sep 1963, *Stauffer & Jacot-Guillarmod 5158* (GRA, K, PRE); Andries Vosloo Kudu Reserve 40 km NE of Grahamstown (–BA), 31 Jan 1980, *Palmer 392* (GRA); near Botha's Hill, top of Queens road (–BA), *Britten 5503* (GRA); next to the road about 6 km N of the N2 and R67 junction (on the R67) (–BA), 4 Nov 2018, *Visser, le Roux & Simali 368* (PRE); Penrock farm 8–10 mi. [12.9–16.1 km] from Grahamstown (–BA), Sep 1926, *Dyer 595* (GRA); Grahamstown Nature Reserve (–BC), 20 Sep 1963, *Jacot-Guillarmod 6838* (GRA); Alexandria District, Kolsrand (–CA), 21 Feb 1952, *Archibald 4010* (GRA, K, PRE); Albany, between Narraway and Longford Grange, Alexandria road, beginning of Bushmans River Valley (–CB), 23 Oct 1955, *Martin 8455* (GRA); SW of Grahamstown, between Narraway and Longford-Grange (–CB), 23 Sep 1963, *Stauffer & Jacot-Guillarmod 5208* (GRA, K); Bathurst, Kariega Park near R343, about 16 km N of Kenton-on-Sea (–DA), 17 Sep 1994, *Burrows 4119* (GRA); Kariega mouth, left bank of river (–DA), 5 Jul 1955, *Acocks 18,349* (GRA, K); Kenton-on-Sea, Kenton Eco Estate, grasslands next to the coast just East of the Kariegarivier mouth (–DA), 4 Nov 2018, *Visser, le Roux & Simali 372* (PRE); Mr. L. Sinclair's House at Kasuka, on hill overlooking ocean (–DA), 10 Oct 1971, *Dahlstrand 2876* (GRA, NBG, PRE); Kowie District, road to Three Sisters about 5 mi [8 km] from Kowie (–DB), 25 Sep 1918, *Britten 724* (GRA, PRE). **3327 (Peddie)**: Drift Police Post, near road junction to drift (–AC), 12 Mar 1994, *Phillipson 4232* (GRA); Fish River Mouth (–AC), 21 Feb 1981, *Phillipson 169* (K); East London District, Christmas Rock, edge of dune forest (–BA), 20 Nov 1961, *Acocks 21,838* (K, PRE). **3424 (Humansdorp)**: Jeffreys Bay (–BB), Jul 1927, *Duthie 1088* (NBG); Sep 1928, *Fourcade s.n.* (NBG); 23 Sep 1998, *Brown 98/09/23/PB/78* (GRA); Welbedacht Division, Humansdorp (–BB), Sep 1909, *Fourcade 447* (K).

3. *Thesium junceum* Bernh. in C.Krauss, Flora 28(5): 80 (1845); A.DC. in Prodr. 14: 669 (1857) partly; A.W.Hill in Dyer, Fl. Cap. 5(2): 174 (1925); Goldblatt and J.C.Manning in J. S. African Bot. Suppl. 13: 407 (1984); Bond and J.C.Manning in Strelitzia 9: 641 (2000); J.C.Manning and Goldblatt in Strelitzia 29: 728 (2012); Bredenk. and Germish. in Bredenk., Strelitzia 41(2): 1462 (2019). *Linosyris juncea* (Bernh.) Kuntze in Revis. Gen. Pl. 2: 588 (1891). Type: South Africa, Eastern Cape, Willowmore (3323): in Zitzikamma [Tsitsikamma] (–DD), Feb 1839, *Krauss 1804* (TUB000206, lecto. – image!, designated here; FI – image!, G, M – image!, TUB [2 sheets] – images!, W – image!, isolecto.; K – fragment!). [*Note: Krauss 1804* (TUB) was selected as the

lectotype of this species as it contains an entire plant, and also shows variation in the habit.]

T. junceum Bernh. var. *mammosum* A.W.Hill in Bull. Misc. Inform. Kew 1: 33 (1915), **syn. nov.**; A.W.Hill in Dyer, Fl. Cap. 5(2): 174 (1925). Type: South Africa, Eastern Cape, Port Elizabeth (3325): near Port Elizabeth, Walmer (–DC), Oct 1909, *Paterson 806* (K000431643, lecto.!, designated here; GRA!, isolecto.). [*Note*: The lectotype of this taxon is selected as *Paterson 806* (K) because it shows the distinguishing characteristics of the taxon and is annotated by Hill.]

T. junceum Bernh. var. *plantagineum* A.W.Hill in Bull. Misc. Inform. Kew 1: 33 (1915), **syn. nov.**; A.W.Hill in Dyer, Fl. Cap. 5(2): 174 (1925). Type: South Africa, Eastern Cape, Butterworth (3228): near Qolora [Zolora] River Mouth (–CB), Jan 1909, *Pegler 1302* (K000431644, lecto.!, designated here; BM!, GRA!, K!, isolecto.). Other original material: South Africa, Eastern Cape, Butterworth (3228): Transkei, Kentani (–CB), Jan 1909, *Pegler 878* (K, syn.!; PRE, syn.!). [*Note: Pegler 1302* (K) was selected as the lectotype of *T. junceum* var. *plantagineum* as it is of good quality with ample material for study and shows an entire plant. It is also named and annotated by Hill.]

Slender to robust perennial herb, up to 0.5 m tall, divergent to erect (virgate). *Stems* 1–21(40) at ground level, branched from the lower third upwards. *Leaves* scale-like, linear to ovate-triangular to rhombic-ovate, 0.5–3.5 × 0.5–1.2 mm long, apices acute to acuminate, margins erose and slightly cartilaginous. *Inflorescences* up to 225 mm long with 4–132 flowers, usually with one fertile flower and two bracteoles in each bract but sometimes with sterile bracts (appearing as vegetative growth), 2–14 flowers per cm in the middle of the inflorescence. *Bracts* ovate-rhomboid, 1.3–2.5 × 0.9–1.9 mm, apices acute to strongly acuminate, margins erose and clearly cartilaginous, bract apices reaching beyond the flower lobe sinuses; bracteoles similar to bracts but sometimes slightly larger. *Flowers* 2.0–3.7 mm long, corolla lobes 0.6–1.1 mm long, densely bearded at the apex and with long hairs all along the lobe margins, apices hooded, hoods 0.2–0.5 mm long, flat disc absent. *Anthers* entirely inserted in the tube, 0.4–0.6 mm long. *Stigmas* sessile to subsessile (styles 0–0.1 mm long), reaching to the bottom of the anthers. *Fruits* 3.4–4.2 mm long, stipes 0.3–0.6 mm long, fruits without perianth 2.0–2.8 × 1.6–2.3 mm.

Distribution and ecology

Thesium junceum is endemic to South Africa, where it occurs at altitudes between 30 and 2340 m a.s.l. from Victoria Bay in the Western Cape to the Drakensberg Garden area in KwaZulu-Natal (Fig. 6B). This species is found in grasslands and open grassy areas in fynbos, heathland, sourveld and thornveld. It occurs on a variety of soil types including clay, sand, loam and rocky or humus rich soils, often on sandstone and occasionally on dolerite and quartzite. *Thesium junceum* flowers between July and April.

Diagnostic characters

Thesium junceum might be confused with *T. paronychioides* when plants grow ascending-erect with a single stem branching into multiple stems shortly above ground level (characteristic of *T. paronychioides*). *Thesium junceum* however differs from *T. paronychioides* in the shorter corolla apex hoods (0.2–0.5 mm long), dense beard on the corolla lobe apices (Fig. 3B) and the longer inflorescences (up to 225 mm long) with 4–132 flowers [longer corolla lobe apex hoods (± 0.6 mm long), sparsely papillate corolla lobe apices and shorter inflorescences (up to 70 mm long) with 18–29 flowers in *T. paronychioides*]. *Thesium junceum* plants that grow erect and branch from the middle third upward might also be confused with *T. natalense*. *Thesium junceum* differs in the shorter inflorescences (up to 225 mm long) with 2–14 flowers per cm in the middle of the inflorescence, the frequent presence of sterile bracts, bract margins that are invariably broadly cartilaginous, and shorter corolla lobes (0.6–1.1 mm long) with a dense beard at the apices and long hairs on the lower margins (Fig. 3B) [longer inflorescences (up to 380 mm long) with 2–5 flowers per cm in the middle of the inflorescence, absence of sterile bracts, bract margins that are scarcely cartilaginous, if at all, and longer corolla lobes (1.2–1.7 mm long) with a dense beard at the apices and shorter hairs on the lower margins in *T. natalense*]. *Thesium junceum* plants occurring at high altitudes (1350–2340 m a.s.l.) between Maclear in the Eastern Cape and the Drakensberg Garden area in KwaZulu-Natal often have a somewhat stunted appearance and more condensed inflorescences.

Three varieties of *T. junceum* are currently recognised (*T. junceum* var. *junceum, T. junceum* var. *mammosum* and *T. junceum* var. *plantagineum*), but we propose that *T. junceum* var. *mammosum* and *T. junceum* var. *plantagineum* are reduced into synonymy under *T. junceum*. Hill (1915, 1925) described *T. junceum* var. *plantagineum* as a new taxon characterised by "dense spikes resembling those of *Plantago maritima*". Based on type material and taxon descriptions, two groups initially seemed evident when examining ca. 60 *T. junceum* specimens: *T. junceum* var. *plantagineum* (group 1) and *T. junceum* var. *junceum* (group 2). Plants in group 1 had relatively denser inflorescences and grew erect to virgate with only a few stems [ca. 1–6(11)] at ground level that branch from the middle third upwards. Conversely, plants from group 2 had relatively less dense inflorescences and grew divergent-erect with multiple stems [ca. 1–21(40)] at ground level that branch from the lower third upwards. However, it became very difficult and arbitrary to separate plants with 'denser' inflorescences as no definitive line could be drawn between specimens with dense and less dense inflorescences. In an effort to identify clear diagnostic character(s), we recorded several quantitative inflorescence characters for both groups. Plants from group 1 had inflorescences up to 180 mm long with 7–132 flowers and 3–14 flowers per cm in the middle of the inflorescence, while plants from group 2 had inflorescences up to 225 mm long with 12–97 flowers and 3–9 flowers per cm in the middle of the inflorescence. It is likely that inflorescence characters, amongst others, vary according to plant age, inflorescence age and the effects of grazing, burning, altitude and other in situ conditions. This variation may not have been evident to Hill (1915, 1925) when describing *T. junceum* var. *plantagineum* as he only cited two specimens for this taxon in his revision and six specimens for *T. junceum* var. *junceum*. We considered that plant habit, number of stems and branching pattern might provide additional diagnostic characters to separate *T. junceum* var. *plantagineum* from *T. junceum* var. *junceum* as discussed earlier. However, upon investigation of an additional ca. 30 specimens from the Selmar Schönland Herbarium (GRA) in Grahamstown it became clear that the before mentioned differences in habit were not absolute and insufficient to separate these two varieties. We therefore propose that *T. junceum* var. *plantagineum* be reduced to synonymy under *T. junceum* based on (1) overlapping inflorescence characters and (2) the absence of other consistent diagnostic characters to support its retention as a distinct taxon.

Thesium junceum var. *mammosum* is separated from the other two varieties of *T. junceum* based solely on the presence of a fleshy protuberance on the inner surface of each corolla lobe, between the apical beard and the corresponding anther (Hill, 1915; Fig. 4). Considering that (1) Hill (1915) described this taxon from only one specimen [*Paterson 806* (K)] and (2) that these lobe protuberances are unique to *T. junceum* var. *mammosum* within this group (see *3.2. Reproductive characters*), further investigation was needed to verify the consistency and reliability of this character. During our examination of ca. 90 *T. junceum* specimens, we found four additional gatherings with similar lobe protrusions [*Balarin 34* (GRA); *Dahlstrand 438* (GRA); *Holland 3878* (GRA, K); *Paterson 681* (GRA)]. The protrusions varied considerably among specimens, from barely visible [*Dahlstrand 438* (GRA)] to very prominent [*Paterson 806* (K, holotype)] which casts

doubt on its reliability as a diagnostic character. As with *T. junceum* var. *plantagineum* this variability may not have been evident to Hill (1915) as he likely only examined a few *T. junceum* specimens. It should be noted that all five gatherings of *T. junceum* var. *mammosum* were collected in the vicinity of Port Elizabeth in the Eastern Cape (3325CD and 3325DC), indicating that it might be a local variant. However, plants of the five known gatherings are considerably dissimilar in general appearance and no additional diagnostic characters could be found, neither in the literature nor in practice, to support upholding *T. junceum* var. *mammosum*. Consequently, we propose that *T. junceum* var. *mammosum* be reduced to synonymy under *T. junceum*.

Conservation status

Thesium junceum is locally abundant and therefore appropriately classified as Least Concern (Raimondo et al., 2009; IUCN Standards and Petitions Subcommittee, 2017). The taxa *T. junceum* var. *mammosum* and *T. junceum* var. *plantagineum*, currently listed as data deficient due to taxonomic problems (Raimondo et al., 2009), are now treated as a synonyms of *T. junceum*.

Additional specimens examined

South Africa. KWAZULU–NATAL: **2929 (Underberg)**: Bushman's Nek, Ngwangwe valley, 14 Jan 1969, *Killick & Vahrmeijer 3941* (K); Bushman's Nek, Thamattue Cave (–CC), 6 Feb 1976, *Hilliard & Burtt 9009* (K, NU); upper Umzimouti [Mzimude] valley (–CC), 26 Nov 1976, *Hilliard & Burtt 9359* (K, NU); Drakensberg Garden reserve, *partie amont de la riviere Umzimkulu* [upstream part of the Umzimkulu river] (–CD), 7 Feb 1982, *Lambinon & Reekmans 82/363* (PRE).

WESTERN CAPE: **3323 (Willowmore)**: Knysna, Paardekop (–CC), 12 Nov 1949, *Steyn 717* (NBG); Uniondale, Lauterwater (–DC), 18 Dec 1933, *Compton 4602* (NBG); 26 Jan 1941, *Compton 10,492* (NBG).

EASTERN CAPE: **3028 (Matatiele):** Maclear District, Naudes Nek Pass, farm Glen Lynden 23, ± 18 km ENE of Rhodes (–CA), 18 Jan 2019, *Bester 14,649* (PRE); Maclear area, grassland patch between PG Bison plantations, Killarney section (–CD), 31 Oct 2018, *Visser, le Roux & Simali 355* (PRE); *356* (PRE). **3128 (Umtata)**: near Ugie, midslopes of the Prentjiesberg (–AA), 11 Nov 2000, *Potgieter 321* (NU). **3226 (Fort Beaufort)**: Stockenstrom District, Katberg near "The Gorge" (–BC), Nov 1926, *Dyer 742* (GRA, K); Stockenstrom District, Katberg Pass (–BC), 24 Jan 1979, *Hilliard & Burtt 12,362* (NU). **3227 (Stutterheim)**: Queenstown Division, Gwatyu farm, mountain side (–AB), 16 Dec 1911, *Galpin 8321* (PRE); S of Cathcart, near Thomas River (–AD), 22 Mar 1996, *Victor 1910* (PRE); Kaffraria, Mount Coke (–CD), Nov 1892, *Sim 1430* (NBG); King Williams Town, Kei road, Stockton farm (–DA), 4 Dec 1957, *Comins 1777* (GRA); hills near Komgha (–DB), Feb 1891, *Flanagan 564* (PRE, SAM); King Williams Town Division, 1 mi. [1.6 km] W of Berlin (–DC), 13 Dec 1958, *Acocks 20,098* (PRE). **3228 (Butterworth)**: Idutywa District (–AB), 18 Feb 1929, *Galpin 10,921* (PRE); Transkei, Willowvale District, *Ngqaqini admin gebied* [admin area] (–AD), Nov 1983, *Van Eeden B 401* (PRE); about 2.2 km SW of Kei Mouth (–CB), 24 Jan 2016, *Bester 13,402* (PRE); about 3 km SW of Kei Mouth (–CB), 23 Jan 2016, *Bester 13,374* (PRE); Kei Mouth (–CB), Apr, *Wager s.n.* (PRE 52,805) (PRE); Komga District, Kei Mouth, farm 106 W of airstrip (–CB), 25 Mar 2014, *Bester 11,904* (PRE); East London, Gonubie (–CC), Sep 1929, *Dyer 2051* (GRA); *Dyer 2057* (K); Komga District, Haga-Haga (Mr. R. Ratley's farm) (–CC), 15 Dec 1977, *Hilliard & Burtt 11,069* (K, NBG, NU). **3324 (Steytlerville)**: Akkerdal (–CB), 28 Jan 2003, *Bredenkamp 1679* (PRE); Honeyville, N Humansdorp on W side of Humansdorp/Andrieskraal road, gate on the W side of the fork in the road (–DD), 9 Jul 2010, *Logie FBG579* (GRA); Humansdorp, Honeyville (–DD), 7 Dec 1979, *Cowling 1388* (GRA). **3325 (Port Elizabeth)**: Somerset East, Zuurberg (–BC), 30 Nov 1947, *Compton 20,260* (NBG); Uitenhage Division, Coega Catchment, Uitenhage 236 farm (–CB), 21 Sep 1974, *Scharf 1615* (PRE); Van Stadens River Wild Flower Reserve E of Port Elizabeth, W facing hillside overlooking the Van Stadens River (–CC), 1 Dec 2007, *Garcia & Lopez Gonzalez MAG3970* (NBG); Van Stadens Wild Flower Local Nature Reserve, on W side of the reserve, by the picnic site (–CC), 8 Mar 2020, *Lombard & Carpenter-Kling 428* (PRE); Greenbushes railway crossing (–CD), 25 Sep 1932, *Holland 3878* (GRA, K); Kragga Kama road (–CD), 30 Aug 1966, *Dahlstrand 438* (GRA); Witteklip (–CD), 31 Jul 1932, *Long 651* (K *partly*); Alexandria, Bushman's River Mouth (–DA), 12 Feb 1953, *Archibald 5054* (GRA); Baakens River, Fern Glen (–DC), 6 Aug 1974, *Olivier 1116* (NBG); near Walmer (–DC), Jul 1915, *Paterson 681* (GRA). **3326 (Grahamstown)**: Faraway, portion 3 of Coldsprings (–AD), 13 Jun 1981, *Jacot-Guillarmod 8589* (GRA); 12 Sep 1981, *Jacot-Guillarmod 8768* (GRA); 7 Nov 1982, *Jacot-Guillarmod 9099* (GRA); Grahamstown (–BC), Oct 1906, *Daly 902* (GRA); Grahamstown Nature Reserve (–BC), 1951, *Martin 9375* (GRA); 20 Sep 1963, *Stauffer, Jacot-Guillarmod and Wells 5187* (GRA, K); Mountain Drive (–BC), 2 Oct 1976, *Bayliss 7636* (NBG, PRE); near Grahamstown (–BC), *MacOwan 690* (GRA, K); Stone's Hill (–BC), Sep 1888, *Galpin 80* (GRA, PRE); 18 Oct 1931, *Rennie & Rennie 175* (GRA); Albany Division, 9 mi [14.5 km] from Rangemore on Grahamstown road (–BD), 21 Jul 1946, *Story 1288* (PRE); Round Hill (Oribi Reserve) (–BD), 11 Apr 1988, *Wirminghaus 192* (GRA); Trappe's valley (–BD), Dec 1903, *Daly 656* (K); Alexandria District, N side of Alexandria (–CB), 24 Jan 1955, *Acocks 17,884* (K). **3327 (Peddie)**: Bathurst Division, near Rangemore (–AC), *Burchell 3868* (K); East London (–BB), Oct 1962, *Bokelmann 2 (Plate 47)* (NBG); 1888, *Thode 6591* (NBG); East London, Ovutan(?), 11 mi. [17.7 km] W of East London (–BB), Dec 1918, *Hilner 176* (GRA); East London, Shelly Beach (–BB), 27 Jan 1979, *Hilliard & Burtt 12,413* (K, NU); East London, W bank, Potter's Pass (–BB), 13 Dec 1981, *Hilliard & Burtt 14,820* (K, NU, PRE); 30 Apr 1982, *Jacot-Guillarmod & Brink 27* (GRA); Fish Point (–CA), Apr 1946, *Pocock 2096* (GRA). **3424 (Humansdorp)**: Humansdorp Division, S slope of Kareedouw Pass (–AA), 12 Aug 1943, *Fourcade 6058* (NBG); Kareedouw Pass (–AA), 13 Oct 1928, *Gillett 1518* (NBG); Rob Hoek flats (–AA), Aug 1921, *Fourcade 1387a* (K *partly*, NBG); Humansdorp Division, Hofmansbosch (–AB), 31 Dec 1918, *Britten 1043* (GRA); Kruisfontein (–BA), 11 Sep 1897, *Galpin 4551* (GRA, K). Cape Province, without precise locality, Jan 1930, *Ryder 97* (K); *Flanagan 394* (PRE).

4. *Thesium lisae-mariae* Stauffer in Markgr., Vierteljahrsschr. Naturf. Ges. Zürich 114(1): 77 (1969); Bredenk. and Germish. in Bredenk., Strelitzia 41(2): 1458 (2019). Type: South Africa, Eastern Cape, Grahamstown (3326): Albany district, farm Slaaikraal, 6 engl. meilen [9.7 km] WNW of Grahamstown (–AD), 18 Sep 1963, *Stauffer, Jacot-Guillarmod & Wells 5173* (Z-000028046, holo. – image!; GRA!, K!, PRE!, iso.).

Suffrutex, up to 0.8 m tall, decumbent to ascending-erect. *Stems* multiple at ground level, branched from the lower third upwards. *Leaves* scale-like, linear (ovate), (1.0)1.5–2.5 × 1.0–1.2 mm long, apices acuminate, margins entire to erose and dying back light brown but usually not cartilaginous. *Inflorescences* up to 180 mm long with 22–31 flowers, usually with one, rarely to three fertile flowers, and two bracteoles in each bract, 3–7 flowers per cm in the middle of the inflorescence. *Bracts* (rhombic)ovate, ± 1.4–1.7 × 1.0–1.5 mm, apices acute to acuminate, margins entire to erose and somewhat cartilaginous, bract apices reaching to middle of flower lobes; bracteoles similar to bracts but smaller. *Flowers* 1.7–2.3 mm long, corolla lobes 0.5–0.7 mm long, glabrous or verrucous at the apex, apices slightly hooded, hoods ± 0.3 mm long, flat disc present. *Anthers* entirely exerted from the tube, ± 0.3 mm long. *Stigmas* subsessile, below or reaching to the lower half of the anthers. *Fruits* ± 4.5 mm long, stipes ± 1 mm long, fruits without perianth ± 3.7 × 2.8 mm.

Distribution and ecology

Thesium lisae-mariae is endemic to South Africa. It is currently known from only two collections in the vicinity of Grahamstown in

the Eastern Cape (Fig. 6C). Little is known about its habitat but it has been recorded to occur alongside *Bobartia* and *Restio* plants. *Thesium lisae-mariae* has been collected in flower in September and November at altitudes between 550 and 650 m a.s.l.

Diagnostic characters

Within the *T. scirpioides* complex, *T. lisae-mariae* is most similar to *T. atratum*. Both these species are easily separated from other species in the complex by the presence of a flat disc at the base of the perianth tube, as well as the absence of hairs or papilla on the corolla lobe apices and margins. *Thesium lisae-mariae* differs from *T. atratum* in its few-flowered inflorescences (22–31 flowers per inflorescence) with sparsely arranged flowers (3–7 flowers per cm in the middle of the inflorescence), brown bracts (when dry, likely green when fresh) with cartilaginous margins and shorter fruit stipes (± 1 mm long) [versus many-flowered inflorescences [(34)47–116 flowers per inflorescence] with flowers arranged close together (5–17 flowers per cm in the middle of the inflorescence), very dark or black bracts with non-cartilaginous margins and longer fruit stipes ((1.2)1.5–2.0 mm long) in *T. atratum*]

Conservation status

This species is currently classified as data deficient due to taxonomic problems (Raimondo et al., 2009) and requires a reassessment. It is currently known from two localities with an extent of occurrence (EOO) of 0 km^2 and area of occupancy (AOO) of 8 km^2. The small number of collections of this species might be an artefact of its non-descript appearance, so that it is easily overlooked, rather than an indication of its rarity. Although several natural areas encircle its distribution range, the presence of this species in its natural habitat has not been verified in recent times. Further population level studies of *T. lisae-mariae* are also needed to assess Criteria A, C, D and E. Therefore, based on available data we suggest a preliminary conservation status of Endangered (EN) under Criterion B (IUCN Standards and Petitions Subcommittee, 2017).

Additional specimens examined

South Africa. EASTERN CAPE: **3326 (Grahamstown)**: Grahamstown (–BC), Nov 1923, *Rogers 27,445* (GRA).

5. *Thesium natalense* Sond. in Flora 40(23): 358 (1857); A.W.Hill in Dyer, Fl. Cap. 5(2): 174 (1925); N.E.Br. in Burtt Davy, Man. Pl. Transvaal 2: 451 (1932). Type: South Africa, KwaZulu-Natal, Pietermaritzburg (2930): ad Port Natal [near Durban] (–DD), *Gueinzius s.n.* (S09–2861, lecto. – image!, designated here; G, isolecto.; K – fragment!). [*Note: Gueinzius s.n.* (S) was selected as the lectotype of *T. natalense* as it contains an entire plant that clearly shows the habit of the species. It is also housed in S where many of Sonder's types are kept and it is therefore likely that the species was described from this specimen.]

Slender perennial herb, up to 0.75 m tall, erect. *Stems* 1–3 at ground level, branched from the middle third upwards. *Leaves* scale-like, linear(linear-elliptic), 0.8–2.8 × 0.2–1.0 mm long, apices acuminate(acute), margins entire or sometimes erose but not cartilaginous. *Inflorescences* up to 380 mm long with 17–89 flowers, usually with one fertile flower and two bracteoles in each bract, 2–5 flowers per cm in the middle of the inflorescence. *Bracts* lanceolate to ovate (rarely rhomboid), 1.1–2.4 × 0.6–1.2 mm, apices acuminate, margins erose and sometimes scarcely cartilaginous, bract apices reaching beyond the flower lobe sinuses; bracteoles similar to bracts but slightly smaller. *Flowers* 2.4–4.5 mm long, corolla lobes 1.2–1.7 mm long, densely bearded with long hairs at the apex and with shorter hairs on the lower margins, apices slightly hooded, hoods 0.2–0.3 mm long, flat disc absent. *Anthers* entirely inserted in the tube, 0.3–0.5 mm long. *Stigmas* sessile to subsessile (styles 0–0.3 mm long), reaching to the lower half of the anthers. *Fruits* 3.7–5.2 mm long, stipes 0.4–0.9 mm long, fruits without perianth 2.2–3.4 × 1.8–2.6 mm.

Distribution and ecology

Thesium natalense is endemic to South Africa, where is occurs from Hluhluwe Game Reserve (KwaZulu-Natal) south-eastwards to Clydesdale, Griqualand (KwaZulu-Natal) and south-eastwards again to the Mkambati Nature Reserve (Eastern Cape) (Fig. 6D). It is found on sandy or rocky soils (often on sandstone) in grasslands and sourveld between 25 and 760(1145) m a.s.l. Flowering time is between (August)September and February.

Diagnostic characters

Thesium natalense is similar to *T. scirpioides* but differs in its taller, slender habit, up to 0.75 m tall, with 1–3 stems branched from the middle third upwards (Fig. 2G), 2–5 flowers per cm in the middle of the inflorescence and smaller fruits (without perianth) 2.2–3.4 × 1.8–2.6 mm (shorter, rush-like habit, up to 0.35 m tall, 1–17 stems that are unbranched or branched from the lower third upwards, 0–2 flowers per cm in the middle of the inflorescence and larger fruits (without perianth) 3.5–5.1 × 2.4–3.6 mm in *T. scirpioides*). It is also similar to *T. junceum* but the inflorescences are longer (up to 380 mm long) with 2–5 flowers per cm in the middle of the inflorescence, it never has sterile bracts, the bract margins are only scarcely cartilaginous, if at all, and the corolla lobes are longer (1.2–1.7 mm long) and have a dense beard at the apices and shorter hairs along the lower margins (Fig. 3F) [shorter inflorescences (up to 225 mm long) with 2–14 flowers per cm in the middle of the inflorescence, sterile bracts often present, bract margins invariably broadly cartilaginous, and shorter corolla lobes (0.6–1.1 mm long) with a dense beard on the apices and long hairs along the lower margins in *T. junceum*].

Conservation status

Thesium natalense is locally abundant and therefore appropriately classified as Least Concern (Raimondo et al., 2009; IUCN Standards and Petitions Subcommittee, 2017).

Additional specimens examined

South Africa. KWAZULU–NATAL: **2730 (Vryheid)**: Pivaanspoort NW of Vryheid (–CB), 2 Dec 1999, *Scott-Shaw 9752* (NU). **2731 (Louwsburg)**: Nongoma District, 10 Oct 1943, *Gerstner 4702* (K). **2832 (Mtubatuba)**: Hlabisa District, Hluhluwe Game Reserve (–AA), 14 Nov 1982, *Phelan 654* (NU). **2930 (Pietermaritzburg)**: Pietermaritzburg, Greytown road (–BA), 13 Sep 1974, *Smook 588a* (K, NU); Hermannsburg School Nature Reserve (–BB), 20 Oct 2001, *Scott-Shaw 11,109* (NU); Mshwati, Noodsberg, R614 to Noodsberg Mill, E for 8 km and N for 8 km, turn right on district road into the valley for 1 km, the grassland below the road after the cattle gate, Marshmont farm (–BD), 29 Oct 2018, *Young 3030* (NU); Hawthorns Hills (–CB), 23 Sep 1944, *Allsopp 435* (NU); Ingomankulu, Hope farm, Umlaas Road (–CB), 9 Sep 2007, *Young 547* (NU); near Thornville, Maritzburg [Pietermaritzburg] (–CB), 6 Oct 1945, *Acocks 11,841* (PRE); Woodlands, Maritzburg [Pietermaritzburg] (–CB), 20 Nov 1944, *Allsopp 539* (NU); between Monteseel and Valley of 1000 hills (–DA), *Edwards 252* (NU); Harrison Flats (–DA), 20 Sep 2004, *Scott-Shaw s.n.* (NU); Inchanga (–DA), 6 Oct 1917, *Bews 922* (NU); Inanda (–DB), Nov 1883, *Medley-Wood 168* (K, SAM); *242* (K, SAM); Bothas Hill (–DC), 3 Sep 1930, *Hutchinson 4726* (K); M. Stainbank's farm, mid-Illovo (–DC), 10 Dec 2008, *Young 871* (NU); Clairmont, 16 mi [25.7 km] (–DD), 1893, *Schlechter 3064* (BM, K, NBG, PRE); 31 Aug 1893, *Medley-Wood 4920* (SAM); Kloof, Spy Hill (–DD), Nov 2001, *Styles s.n.* (NU); Krantzkloof (–DD), Oct 1921, *Haygarth 24,640R* (PRE); Krantzkloof Nature Reserve (–DD), 26 Oct 2001, *Styles 51* (NU); Pietermaritzburg, Pinetown, Umbilo River valley (–DD), 13 Jan 1972, *Ward 7523* (NU, PRE);

Pinetown District, Westville (–DD), 22 Sep 1965, *Moll 2323* (NU); St. Helier farm, near Gillits grasslands at top facing sea, below saw dust dump (–DD), 1 Nov 2003, *Scott-Shaw 13,071e* (NU); *Scott-Shaw 13,074e* (NU); Umlaas Filters, Durban Corporation property (–DD), 22 Oct 1981, *Schrire 623* (NH); Umlazi (–DD), 19 Dec 1987, *Cunningham 2735* (NU). **2931 (Stanger)**: Lower Tugela District, Groutville (–AD), 14 Oct 1965, *Moll 2567* (NU, PRE); Eshowe, Gingindlovu (–BA), 1 Dec 1937, *Gerstner 2453* (K, PRE); Mtunzini District, Amatikulu Nature Reserve (–BA), 5 Dec 2015, *Bester 13,017* (PRE); Mtunzini District, leper institute road (–BA), 23 Sep 1962, *Johnson 1455* (K); Tugela mouth (–BA), Dec 2005, *Edwards 3109* (NU). **3029 (Kokstad)**: Griqualand, Clydesdale (–BD), 1884, *Tyson 2590* (SAM). **3030 (Port Shepstone)**: Alexandria Division, Dumisa Station, Umgoye (–AD), 1909, *Rudatis 721* (BM); Friedenau, Umgaye flat, Alexandra city (–AD), 30 Sep 1909, *Rudatis 502* (NBG); Kenterton N.P. (–AD), Aug 1913, *Thode 4815* (NBG); Ifafa Beach, Elysium(?) (–BC), 1 Oct 1992, *Goodall s.n.* (NU); Umzinto, Vernon Crookes Nature Reserve (–BC), 2 Oct 1983, *Balkwill & Manning 978* (NU); 30 Sep 1984, *Balkwill & Cadman 2064* (NU); 3 Oct 1992, *Voss 433* (NU); 5 Oct 1992, *Edwards 1133* (K, NU, PRE); on St. Faiths road (–CA), 5 Jul 1938, *Hafström & Acocks 477* (PRE); Port Shepstone District, Oribi Falls escarpment (–CB), 29 Dec 1936, *Mogg 13,352* (PRE); Umtamvuna Nature Reserve, 4 km upstream (–CC), 26 Feb 1983, *Balkwill & Manning 415* (NU). **3130 (Port Edward)**: Rennies Beach, 1.55 km from the bridge over the Mtamvuna River, on the KZN side, next to the highway on the ocean side (–AA), 2 Feb 2017, *Visser, le Roux & Nickrent 267* (PRE); Rennies Beach, the red desert 0.56 km SE of the entrance in Maurice road (–AA), 1 Feb 2017, *Visser, le Roux & Nickrent 256* (PRE); Rennies Beach, the red desert, in grassland patch 0.74 km SSE from entrance in Maurice Road, 40 m from the edge of the forest surrounding the Umtamvuna River (–AA), 1 Feb 2017, *Visser, le Roux & Nickrent 257* (PRE); Umtamvuna River, Beacon Hill farm above cliffs (–AA), 15 Dec 1976, *Nicholson 1688* (PRE).

EASTERN CAPE: **3130 (Port Edward)**: Port Edward (–AA), 16 Oct 1969, *Ward 6638* (NU); Red Dune Desert Nature Reserve, grassland next to Red Desert (–AA), 16 Dec 2017, *Young 2877* (NU); Umtamvuna Nature Reserve, Western Heights (–AA), 16 Oct 1995, *Scott-Shaw 7201* (NU); *Scott-Shaw 7195* (NU); Mkambati Nature Reserve (–AC), 16 Jan 1997, *Makwarela 239* (PRE); 1 Oct 1984, *Shackleton 21* (PRE).

6. *Thesium paronychioides* Sond. in Flora 40(23): 359 (1857); A.W. Hill in Dyer, Fl. Cap. 5(2): 175 (1925); Goldblatt and J.C.Manning in J. S. African Bot. Suppl. 13: 407 (1984); Bond and J.C.Manning in Strelitzia 9: 641 (2000); J.C.Manning and Goldblatt in Strelitzia 29: 728 (2012). Type: South Africa, Western Cape, Bredasdorp (3420): Zwellendam (–AB), without date, *Mundt 13* (S07–9312, lecto. – image!, designated here; MO – image!, isolecto.; K – fragment!). [*Note: Mundt 13* (S) is designated as the lectotype of this species as it contains a whole plant, including the rootstock, shows the characteristic branching pattern of the species and is kept in S where many of Sonder's types are housed.]

Annual (short-lived perennial?), up to 0.14(0.25) m tall, ascending-erect. *Stems* 1 at ground level, branched from the lower third upwards. *Leaves* scale-like, linear, 1.2–2.5 × 0.5–0.8 mm long, apices acute, margins entire to erose and cartilaginous. *Inflorescences* up to 70 mm long with 18–29 flowers, usually with one fertile flower and two bracteoles in each bract, 4–6 flowers per cm in the middle of the inflorescence. *Bracts* broadly rhombic-ovate to subcircular, 1.5–1.7 × 1.1–1.4 mm, apices broadly acute to acuminate, margins strongly erose and cartilaginous, bract apices reaching to the middle of the corolla lobes; bracteoles similar to bracts. *Flowers* 2.0–2.3 mm long, corolla lobes ± 0.9 mm long, sparsely papillate at the apex, apices hooded, hoods ± 0.6 mm long, flat disc absent. *Anthers* entirely inserted in the tube, ± 0.4 mm long. *Stigmas* subsessile (styles ± 0.1 mm long), reaching to the bottom of the anthers. *Fruits* 3.3–3.4 mm long, stipe 0.3–0.4 mm long, fruits without perianth 2.1–2.4 × 1.6–1.8 mm.

Distribution and ecology

Thesium paronychioides is endemic to the Western Cape province of South Africa. It has been recorded at altitudes around 180 m a.s.l. between Knysna in the east and Swellendam in the west (Fig. 6E). Flowering time is between October and March.

Diagnostic characters

Thesium paronychioides is similar to *T. flexuosum* but differs in the annual or possibly short-lived perennial ascending-erect habit (Fig. 2H), inflorescences with 18–29 flowers, flowers 2.0–2.3 mm long, corolla lobes ± 0.9 mm long and anthers entirely inserted in the tube (Fig. 3C) (robust, suffrutescent and spreading to erect polymorphic habit, inflorescences with 18–73 flowers, flowers 1.6–3.3 mm long, corolla lobes 0.7–1.6 mm long, and anthers inserted halfway in the tube in *T. flexuosum*). It might also be confused with *T. junceum* when plants grow ascending-erect with a single stem branching into multiple stems shortly above ground level. *Thesium paronychioides* can however be distinguished by the longer corolla lobe apex hoods (± 0.6 mm long), its sparsely papillate corolla lobe apices (Fig. 3C) and shorter inflorescences that are up to 70 mm long with 18–29 flowers [corolla lobe apex hoods 0.2–0.5 mm long and with a dense beard on the corolla lobe apices and longer inflorescences (up to 225 mm long) with 4–132 flowers in *T. junceum*].

Conservation status

Thesium paronychioides is currently listed as Least Concern (Raimondo et al., 2009) but closer study has revealed that it is scarcer than previously thought and therefore requires reassessment. It has an estimated EOO of 1104 km^2, AOO of 20 km^2 and is known from only five localities of which four are historical records (i.e. number of localities 1–5). There has been substantial transformation of natural habitat in this area into urban developments and agricultural practices. A number of established nature reserves likely provide refuge for this species but this has not been verified. Insufficient data is currently available to assess *T. paronychioides* against Criteria A, C, D and E. We therefore suggest a preliminary conservation status of Endangered (EN) under Criterion B (IUCN Standards and Petitions Subcommittee, 2017).

Additional specimens examined

South Africa. WESTERN CAPE: **3322 (Oudtshoorn)**: George (–CD), 29 Mar 1893, *Schlechter 2428* (BM, GRA, K, NGB, PRE); George Division, Victoria Bay (–DC), 19 Oct 1953, *Lewis 5111* (SAM); Ruggle valley near Sedgefield (–DD), Nov 1979, *Hugo 2009* (NBG). **3422 (Mossel Bay)**: Belvidere (Knysna) (–BB), 11 Oct 1931, no collector information (NBG).

7. *Thesium scirpioides* A.W.Hill in Bull. Misc. Inform. Kew 1: 40 (1915); A.W.Hill in Dyer, Fl. Cap. 5(2): 175 (1925); N.E.Br. in Burtt Davy, Man. Pl. Transvaal 2: 459 (1932); Retief and P.P.J.Herman in Strelitzia 6: 599 (1997); Hilliard in Fl. Zambes. 9(3): 241 (2006); Retief and N.L.Mey. in Strelitzia 38: 752 (2017). Type: South Africa, KwaZulu-Natal, Underberg (2929): Mooi River flat (–BB), 28 Nov 1888, *Medley-Wood 4066* (K000431646, lecto.!, designated here; BOL – image!, isolecto.). Other original material: South Africa, Free State, Bethlehem (2828): Besters Vlei, near Witzies Hoek (–DB), Dec, *Bolus 8248* (type not found, syn.). Harrismith (2829): Orange River Colony, Harrismith (–AC), Dec 1904, *Sankey 249* (K, syn.!). Free State, without precise locality, 1862, *Cooper 834* (E, syn. – image!; K, syn!; PRE, syn.!). KwaZulu-Natal, Kokstad (3029): Griqualand East, near Kokstad (–AD), Oct 1883, *Tyson 1535* (K, syn.!). [*Note*: The lectotype of *T.*

scirpioides is designated as *Medley-Wood 4066* (K) as it gives a good representation of the species, shows all diagnostic characters, contains flowers and fruit, and is identified and annotated by Hill.]

Rush-like perennial herb, up to 0.35 m tall, erect-virgate. *Stems* 1–17 at ground level, branched from the lower third upwards or occasionally unbranched. *Leaves* scale-like, linear to ovate(rhombic-ovate), 1–5 × 0.3–1.8 mm long, apices acute(acuminate), margins entire to erose but not cartilaginous. *Inflorescences* up to 160 mm long with 7–22 flowers, usually with one fertile flower and two bracteoles in each bract, 0–2 flowers per cm in the middle of the inflorescence. *Bracts* ovate-rhomboid, 1.6–3.0 × 0.8–1.6 mm, apices acute (acuminate), margins erose and scarcely cartilaginous, bract apices reaching up to the flower lobe sinuses; bracteoles similar to bracts. *Flowers* 3.5–5.0 mm long, corolla lobes 1.4–1.8 mm long, densely bearded with long hairs at the apex and with shorter hairs on the lower margins, apices slightly hooded, hoods 0.1–0.3 mm long, flat disc absent. *Anthers* entirely inserted in the tube, 0.5–0.6 mm long. *Stigmas* ± sessile (styles ± 0–0.1 mm long), reaching to below (or to the bottom of) the anthers. *Fruits* 5.2–7.3 mm long, stipes 0.6–1.0 mm long, fruits without perianth 3.5–5.1 × 2.4–3.6 mm.

Distribution and ecology

Thesium scirpioides occurs in Eswatini, Lesotho, Mozambique and South Africa (Hilliard, 2006). It ranges from Namaacha in Mozambique westwards through Eswatini to Johannesburg in Gauteng, South Africa and from there southwards through the Free State province of South Africa and Lesotho to the Mkambati Nature Reserve in KwaZulu-Natal (South Africa) (Fig. 6F). It occurs on sandy, rocky or loamy soils in grasslands between 350 and 2240 a.s.l. Flowering time is between August and December.

Diagnostic characters

Thesium scirpioides is similar to *T. natalense* but differs in its shorter, rush-like habit, up to 0.35 m tall, 1–17 stems which are unbranched or branched from the lower third upwards (Fig. 2I), 0–2 flowers per cm in the middle of the inflorescence and larger fruits (without perianth) 3.5–5.1 × 2.4–3.6 mm [taller, slender habit, up to 0.75 m tall, with 1–3 stems branched from the middle third upwards, 2–5 flowers per cm in the middle of the inflorescence and smaller fruits (without perianth) 2.2–3.4 × 1.8–2.6 mm in *T. natalense*].

Conservation status

Thesium scirpioides is widespread and abundant, and therefore appropriately classified as Least Concern (Raimondo et al., 2009; IUCN Standards and Petitions Subcommittee, 2017).

Additional specimens examined

South Africa. GAUTENG: **2628 (Johannesburg)**: Melville Koppies (–AA), 20 Sep 1960, *Macnaea 1227* (NBG); near the Zoo (–AA), 5 Dec 1926, *Moss 14,419* (BM); Suikerbosrand Nature Reserve about 20 m into the grassland on the right hand side of the main road, just before the first T-junction (–AC), 12 Dec 2016, *Visser & le Roux 232* (PRE).

MPUMALANGA: **2530 (Lydenburg)**: *Ost-Transvaal, Belfast Division, ± 5 meilen [8 km] nach Machadodorp richtug Schoemanskloof* [East Transvaal, Belfast Division, about 5 mi [8 km] from Machadodorp towards Schoemanskloof] (–CB), 10 Oct 1963, *Stauffer & Weder 5263* (GRA, K, PRE); Carolina, farm Haverfontein 7 IT, Brakfontein road, hilltop 900 m S of railway crossing (–CC), 7 Nov 2009, *Makgakga, Masupa & Nonyane 565* (PRE). **2531 (Komatipoort)**: Barberton District, ± 10 km SW of Barberton, farm Ameide 737, ± 2 km SW of Shokhohlwa Peak (–CC), 15 Nov 2014, *Bester 12,163* (PRE). **2630 (Carolina)**: Carolina (–AA), Dec 1917, *Rogers & Moss 1145* (K *partly*). **2729 (Volksrust)**: 15 km SW of Volksrust, farm Schuilhoek 139 HS (–BD), 30 Nov 2015, *Bester 12,927* (PRE).

FREE STATE: **2828 (Bethlehem)**: about 3 mi [4.8 km] out of village, side of kopje [hill] (–AB), 4 Dec 1919, *Phillips 3224* (K, PRE); Bethlehem (–AB), *Potgieter s.n.* (TRV 21,868) (PRE). **2829 (Harrismith)**: Platberg, Zig-zag path (–AC), 14 Dec 1976, *Hilliard & Burtt 9529* (K, NU); Sterkfontein Dam (–AC), 16 Oct 1974, *Jacobsz 1829* (NBG); *Kerkenberg, skuinste SW aansig bokant kampplek* [SW facing slope above campsite] (–CA), 18 Nov 1981, *Jacobsz 1272* (PRE).

KWAZULU–NATAL: **2730 (Vryheid)**: Utrecht District, Wakkerstroom, Groenvlei, just inside the Natal [KwaZulu-Natal] border (–AC), 3 Nov 1985, *Hilliard & Burtt 18,535* (K, NU). **2828 (Bethlehem)**: Bergville District, Tiger Falls (–DB), 20 Nov 1930, *Schweickerdt 668* (PRE). **2829 (Harrismith)**: Bergville District, Bezuidenhout Pass (–CA), 10 Dec 1976, *Hilliard & Burtt 9455* (NU); Oliviers Hoek Pass (–CA), Dec 1906, *Thode 4187* (NBG); Bergville, Cathedral Peak Research Catchments, uKhahlamba Drakensberg, Cathedral Peak, grassland and sheep permanent monitoring plots: P182 (–CC), 27 Nov 2013, *Gordijn 257* (NU); Bergville District, Cathedral Peak Forest Research Station (–CC), 12 Nov 1951, *Killick 1572* (NU). **2929 (Underberg)**: Impendhle, "Tillietudlem" (–BB), Dec 1948, *Huntley 437* (NU); Mooi River (J.E. Chapman) (–BB), 26 Oct 1918, *Mogg 3183* (PRE); Impendhle District, Loteni Nature Reserve (–BC), 10 Oct 1978, *Phelan 144* (NU); Ukahlamba WHS, Highmoor Nature Reserve, on path to Aasvoël Cave (–BC), 9 Dec 2017, *Young 2730* (NU); Garden Castle Forest Reserve, path in Sleeping Beauty Cave Valley (–CA), 3 Nov 1981, *Hilliard 8168* (NU); Bamboo Mountain; foot of mountain, N side near Umzimkhulwana River (–CB), 22 Nov 1982, *Hilliard & Burtt 15,661* (NU, PRE); Cobham Forest Station (–CB), 10 Nov 1980, *Hilliard & Burtt 13,391* (K, NU, PRE); Sani Pass, N facing slopes (–CB), 14 Dec 1984, *Hilliard & Burtt 17,952* (K, NU); Drakensberg Gardens Forest Station (–CC), 18 Dec 1981, *Schrire 813* (NH, NU); Himeville Nature Reserve, grasslands on either side of entrance road (–DC), 6 Nov 2001, *Scott-Shaw 11,243* (NU); Polela District, Bulwer, Glengariff, Mungay kopjie (–DC), 11 Nov 1974, *Rennie 613* (NU); Sunset farm, Bulwer mountain valley (–DC), 4 Nov 1983, *Rennie 1351* (NU); Watermead farm (–DC), 10 Oct 1988, *Williams 245* (PRE). **2930 (Pietermaritzburg)**: Noodsberg, Newlands farm (–BD), 14 Oct 1989, *Williams 556* (PRE). **3030 (Port Shepstone)**: Umtamvuna Nature Reserve (–CC), 21 Oct 2004, *Abbott 8104* (PCE); Margate (–CD), 3 Aug 1971, *Nicholson 1122* (PRE).

EASTERN CAPE: **3129 (Port St. Johns)**: Mtentu South, Bridge Site Relevé no. 1 (–BB), 10 Sep 2003, *Lubke 4788* (PRE); Pondoland, outside NW edge of Mkambati Nature Reserve, overlooking Mtentu River gorge (–BB), 28 Sep 2005, *Victor 3018* (PRE).

Swaziland. **2632 (Bela Vista)**: Siteki District, ridge E of Mtibhlati River valley, Lubombo mountains (–CA), 23 Nov 2002, *Burrows & Burrows 7900* (PRE).

Lesotho. **2828 (Bethlehem)**: Leribe (–CC), *Dieterlen 620* (PRE, SAM). **2927 (Maseru)**: Roma, Bacher Campus (–BC), 14 Nov 1974, *Schmitz 4536* (PRE).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The following persons and institutions are thanked: the Botanical Education Trust, Bentham-Moxon Trust, Foundational Biodiversity Information Programme [Small Grant number 104931], University of Johannesburg, South African National Biodiversity Institute (SANBI) and National Research Foundation (NRF) of South Africa [Grant number 84442] for funding; the National Herbarium under the SANBI for hosting the study; the NRF for the NRF NEP Grant Biosystematics Microscopy Imaging System used at the Agricultural Research Council [Grant

number: EQP13100452023] and Robin Lyle for her assistance therewith; Daniel Nickrent and Sedzani Simali for assistance in the field; personnel at the herbaria cited for access to collections and assistance during visits; Hugh Glen for assistance with naming the name species, *T. atratum*; Nicola van Berkel for field photos of *T. atratum*.

References

Brenan, J., 1979. Three new species of *Thesium* (Santalaceae) from South Africa. Kew Bulletin 33, 395–397. https://doi.org/10.2307/4110134.

Brown, N.E., Thesium, L., 1932. In: Burtt-Davy, J. (Ed.), South Africa. Longmans, Green and Co., London, pp. 455–462.

De Candolle, A., 1857. Santalaceae. In: De Candolle, A. (Ed.), Prodromus Systematis Naturalis, pp. 619–692. Paris.

García, M.A., Nickrent, D.L., Mucina, L., 2018. *Thesium nautimontanum*, a new species of Thesiaceae (Santalales) from South Africa. PhytoKeys 109, 41–51. https://doi.org/10.3897/phytokeys.109.28607.

Hill, A.W., 1915. The genus *Thesium* in South Africa, with a key and descriptions of new species. Bulletin of Miscellaneous Information 1, 1–43. https://doi.org/10.2307/4115447.

Hill, A.W., 1925. Order CXX. Santalaceae. In: Thiselton-Dyer, W.T. (Ed.), Flora Capensis Volume 5. L. Reeve & Co. LTD, London, pp. 135–212. https://doi.org/10.2307/4107506.

Santalaceae Hilliard, O.M., 2006. Flora Zambesiaca Volume 9. Timberlake, J., Martins, E. (Eds.), 2006. Flora Zambesiaca Volume 9. Royal Botanic Gardens, Kew 227–228.

IUCN Standards and Petitions Subcommittee, 2017. Guidelines for using the IUCN Red list categories and criteria. Version 13. Available from: https://www.iucnredlist.org/resources/redlistguidelines (accessed 24 August 2017)

Leistner, O.A., Morris, J.W., 1976. Southern African Place Names. Annals of the Cape Provincial Museums. Cape Provincial Museums At the Albany Museum. Grahamstown.

Lombard, N., le Roux, M.M., van Wyk, B.-.E., 2019. *Thesium ovatifolium* (Santalaceae), a new species with ovate leaves from KwaZulu-Natal, South Africa. Phytotaxa 405, 263–268. https://doi.org/10.11646/phytotaxa.405.5.5.

Lombard, N., van Wyk, B.-.E., le Roux, M.M., 2020. A review of the ethnobotany, contemporary uses, chemistry and pharmacology of the genus *Thesium* (Santalaceae). Journal of Ethnopharmacology 256, 112745. https://doi.org/10.1016/j.jep.2020.112745.

Mashego, K.S., le Roux, M.M., 2018. A taxonomic evaluation of the *Thesium confine* species complex (Santalaceae). Bothalia 48,. https://doi.org/10.4102/abc.v48i1.2346 a2346.

Moore, T.E., Verboom, G.A., Forest, F., 2010. Phylogenetics and biogeography of the parasitic genus *Thesium* L. (Santalaceae), with an emphasis on the Cape of South Africa. Botanical Journal of the Linnean Society 162, 435–452. https://doi.org/10.1111/j.1095-8339.2010.01032.x.

Nickrent, D.L., García, M.A., 2015. *Lacomucinaea*, a new monotypic genus in Thesiaceae (Santalales). Phytotaxa 224, 173–184. https://doi.org/10.11646/phytotaxa.224.2.4.

Nickrent, D.L., Malécot, V., Vidal-Russell, R., Der, J.P., 2010. A revised classification of Santalales. Taxon 59, 538–558. https://doi.org/10.1002/tax.592019.

Raimondo, D., Von Staden, L., Foden, W., Victor, J.E., Helme, N.A., Turner, R.C., Kamundi, D.A., Manyama, P.A., 2009. Red list of South African plants. Strelitzia 25. South African National Biodiversity Institute, Pretoria, pp. 1–668.

The Angiosperm Phylogeny Group, 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Journal of the Linnean Society 181, 1–20. https://doi.org/10.1111/boj.12385.

Thiers, B., 2019. Index herbariorum, a Global Directory of Public Herbaria and Associated Staff. . New York Botanical Garden's Virtual Herbarium. Available from: http://sweetgum.nybg.org/ih/ (accessed 18 September 2019).

Victor, J.E., Smith, G.F., Van Wyk, A.E., 2015. Strategy for plant taxonomic research in South Africa 2015–2020. SANBI Biodiversity Series, 26. South African National Biodiversity Institute, Pretoria, pp. 1–39.

Victor, J.E., 2020. Research Strategy For Plant Taxonomy 2020-2030. South African National Biodiversity Institute.. https://www.sanbi.org/wp-content/uploads/2020/03/Research-strategy-for-plant-taxonomy-2020-2030.pdf (accessed 18 April 2020).

Visser, N., le Roux, M.M., van Wyk, B.-.E., 2018. A taxonomic revision of the *Thesium goetzeanum* species complex (Santalaceae) from Lesotho. South Africa and Swaziland. South African Journal of Botany 119, 45–62. https://doi.org/10.1016/j.sajb.2018.08.005.

Zhigila, D.A., Verboom, G.A., Stirton, C.H., Muasya, A.M., 2019a. A taxonomic revision of *Thesium* section *Hagnothesium* (Santalaceae) and description of a new species, *T. quartzicolum*. South African Journal of Botany 124, 280–303. https://doi.org/10.1016/j.sajb.2019.05.016.

Zhigila, D.A., Verboom, G.A., Stirton, C.H., Smith, H.J., Muasya, A.M., 2019b. Seven new *Thesium* (Santalaceae) species endemic to the greater Cape Floristic Region, South Africa. Phytotaxa 423, 215–237. https://doi.org/10.11646/phytotaxa.423.4.1.

Zhigila, D.A., Verboom, G.A., Muasya, A.M., 2020. An infrageneric classification of *Thesium* (Santalaceae) based on molecular phylogenetic data. Taxon 69 (1), 100–123. https://doi.org/10.1002/tax.12202.