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A taxonomic revision of the *Thesium goetzeanum* species complex (Santalaceae) from Lesotho, South Africa and Swaziland

N. Visser [a,b,*], M. Marianne le Roux [a,b], B.-E. van Wyk [a]

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

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ABSTRACT

The genus *Thesium* L. is in urgent need of revision and has been identified as a priority genus for taxonomic research in South Africa. The revision of 16 morphologically similar grassland species from Lesotho, South Africa and Swaziland, here referred to as the *T. goetzeanum* complex, is a first step towards a comprehensive revision of the genus. All members of the complex share the following characters: (1) tepals with a prominent apical beard, (2) anthers attached to the perianth tube with post-staminal hairs, (3) stigmas usually not sessile (rarely sessile in *T. gracilarioides* A.W.Hill and *T. gypsophiloides* A.W.Hill), (4) monotelic inflorescences, (5) leaves, bracts and bracteoles leaf-like, not scale-like, (6) stems leafy, not rush-like, and (7) stems and leaves glabrous. A comprehensive study of morphology, type specimens, distribution information, available literature, as well as field observations, indicate that the number of accepted species should be reduced from 16 to 9, including the newly recognised species *T. infundibulare* N.Visser and M.M.le Roux *sp. nov*. The first comprehensive description of *T. procerum* N.E.Br. is also provided. A taxonomic revision of the *T. goetzeanum* complex is presented, including an identification key, updated nomenclature and typifications, descriptions, diagnostic characters, distribution maps and conservation notes for all nine recognised species.

1. Introduction

Thesium L. is a large genus (±350 species) of hemi-parasites that is included in the family Santalaceae (Forest and Manning, 2013; Nickrent and García, 2015; The Angiosperm Phylogeny Group, 2016). The majority of *Thesium* species are concentrated in southern Africa (±180 species), with the remainder occurring in tropical and northern Africa, Europe, Asia and South America (Germishuizen et al., 2006; Forest and Manning, 2013; Nickrent and García, 2015). *Thesium* (including *Kunkeliella* W.T.Stearn and *Thesidium* Sond.) is monophyletic and sister to *Osyridicarpos* A.DC. plus *Lacomucinaea* Nickrent & M.A. García (Der and Nickrent, 2008; Forest and Manning, 2013; Nickrent and García, 2015). The genus comprises hemi-parasitic herbs or shrubs with sessile, linear or scale-like leaves and dry, nut-like fruits (De Candolle, 1857a; Hill, 1915).

Thesium was first described by Linnaeus (1753) and included four species. Later, both De Candolle (1857a, 1857b) and Sonder (1857a) simultaneously, but independently, published reviews on *Thesium*. These publications resulted in many inconsistencies and contradictions in species concepts and classification systems. Sonder (1857b) later published an amendment in an attempt to reconcile some of the conflicting taxonomic information. Hill (1915, 1925) conducted a comprehensive taxonomic study of the southern African species, which also included descriptions of several new species. Hill's circumscription of species were mostly congruent with those of De Candolle (1857a) and Sonder (1857b), although his classification system differed from theirs mostly due to his narrower perception of morphological variation resulting from the limited geographic range of his study (Moore et al., 2010). Molecular studies show that the sections described by Hill are polyphyletic (Moore et al., 2010; Nickrent and García, 2015). Both these studies focussed predominantly on Fynbos species of *Thesium* and therefore little is known about the relationships among other species. It is, however, clear that Fynbos and grassland species form two monophyletic sister clades (Moore et al., 2010; Nickrent and García, 2015). Since the work of Hill, 38 new southern African *Thesium* species have been described (*e.g.*, Brown 1932; Brenan 1979), yet no attempt has been made to amalgamate and evaluate all of the available taxonomic information for the genus. Currently no complete identification key exists, and considerable confusion remains surrounding species concepts and identification. *Thesium* has consequently been identified as a high priority for taxonomic research in South Africa and is in urgent need of a revision (Victor et al., 2015).

Working towards a comprehensive taxonomic revision of the genus, we review a group of 16 morphologically similar grassland species from

* Corresponding author at: Department of Botany and Plant Biotechnology, University of Johannesburg, PO Box 524, Auckland Park 2006, South Africa.
E-mail address: natashavissermail@gmail.com (N. Visser).

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Lesotho, South Africa and Swaziland (see Table 1) referred to here as the *T. goetzeanum* complex. The *T. goetzeanum* complex forms part of section *Barbata* A.W.Hill as delineated by Hill (1925), corresponding to the section *Frisea* Rchb. in the classification systems of De Candolle (1857a) and Pilger (1935) or subgenus *Frisea* (Rchb.) Peterm. of Hendrych (1972). Species in the *T. goetzeanum* complex are distinguished by the following characters: (1) tepals with a prominent apical beard, (2) anthers attached to the perianth tube with post-staminal hairs, (3) stigmas usually not sessile (occasionally sessile in *T. gracilarioides* A.W.Hill and *T. gypsophiloides* A.W.Hill), (4) monotelic inflorescences, (5) leaves, bracts and bracteoles leaf-like, not scale-like, (6) stems leafy, not rush-like, and (7) stems and leaves glabrous (Fig. 1A–D).

The *T. goetzeanum* complex includes some of the most taxonomically problematic species in the genus. The distinctions among species have been blurred by the increased levels of variation now evident from more recent collections, rendering their identification difficult or impossible. This intraspecific variation was not evident to Hill (1915, 1925) and Brown (1932) from the limited material available to them, on which they based their species concepts (Hendrych, 1972; Moore et al., 2010). The difficulties in identifying species are highlighted by the fact that four species in the *T. goetzeanum* complex are currently classified as data deficient due to taxonomic reasons (*T. coriarium* A.W.Hill, *T. junodii* A.W.Hill, *T. mossii* N.E.Br. and *T. vahrmeijeri* Brenan) (Raimondo et al., 2009).

We recognise nine species in the present treatment, reducing seven names to synonymy (see Table 1) as the diagnostic characters on which these taxa were based fall within the range of variation of previously described species. We provide the first comprehensive description of *T. procerum* N.E.Br., which was only briefly described by Brown (1932), and describe one new species, *T. infundibulare* N.Visser and M.M.le Roux.

2. Materials and methods

Morphological characters of ± 430 herbarium specimens of *Thesium* were examined from the collections in BM, BNRH, BOL, J, K, NBG (including SAM), NH, PCE, PRE and PRU. In addition, digital images of type specimens from B, BR, EM, MO, S and W were examined *via* JSTOR Global Plants (https://plants.jstor.org). Details of these images and specimens studied are provided in the treatment of each species.

Fieldwork was conducted at various sites across the Gauteng, Free State, Limpopo, Mpumalanga and KwaZulu-Natal provinces of South Africa between October 2016 and December 2017 in the flowering period of the grassland species of *Thesium* (August–February). Plants were observed and photographed in their natural habitat to record information such as habit, colour of vegetative and reproductive parts, and possible pollinators. Six of the nine species recognised and treated here were studied in the field. Three plants from each population were collected where possible. Specimens collected were deposited in PRE.

Species distributions were determined from locality information supplied on specimen labels and specimens collected during fieldwork. The SANBI gazetteer v. 4 compiled and managed by Powrie (2015) was used to confirm collection localities. Final distribution maps were compiled using ArcMap v. 10.3.1 (ESRI, Inc.). Specimens are cited following the quarter degree grid reference system of Leistner and Morris (1976).

Vegetative and reproductive morphological characters, as well as distribution information, were used to sort specimens into 10 operational taxonomic units (OTU's), which were finally coalesced into 9 species. Three specimens representing the widest range of variation were selected from each OTU, and three measurements taken of each character on each specimen. Floral measurements were taken using ZEN lite software v. 2.0 (Carl Zeiss Microscopy GmbH), to ensure accuracy of measurements below 3 mm. Around 200 flowers were rehydrated for five minutes in "Windolene" (cleaning agent), after which floral dissections were made using a Nikon SMZ 745 T stereo microscope (Nikon Corporation). Photos of vegetative parts, floral parts (including flower cross sections), and fruits were taken using a Zeiss Discovery V8 Stereo microscope, with a Zeiss 60 N–C, 2/3″, 0.63× camera attached and Zeiss ZEN software (Carl Zeiss Microscopy GmbH). Photographs and figure plates were edited using Microsoft Publisher software v. 14.0.7181.5 (Microsoft Corporation).

Suggested conservation statuses are provided according to the guidelines given by the International Union for Conservation of Nature (IUCN Standards and Petitions Subcommittee, 2017) and evaluated in collaboration with Ms. Lize von Staden (South African Threatened Species Program, South African National Biodiversity Institute).

3. Results and discussion

3.1. Diagnostically reliable characters

A combination of nine characters was used to distinguish among species of the *T. goetzeanum* complex. Hill (1925) previously utilised habit, fusion of bracts to pedicels/peduncles, and inflorescence type as diagnostic characters. In addition to these, five more diagnostic characters are newly recognised here: perennial *vs* annual life history, rootstock, presence or absence of vegetative scales, placental column structure, and the presence or absence of fruit stipes. A summary of diagnostic characters is provided in Table 2.

3.1.1. Vegetative morphology

The growth form of species in the *T. goetzeanum* complex is extremely variable (Hill, 1915). Factors such as elevation, fire, grazing,

Table 1
A list of all accepted species in the *Thesium goetzeanum* complex with synonyms. Heterotypic and homotypic synonyms are denoted with = and ≡ respectively. References listed next to previous synonyms refer to the publications where each synonym was instated.

Accepted species	New synonyms	Previous synonyms
1. *T. goetzeanum* Engl.	= *T. coriarium* A.W.Hill	= *T. caespitosum* Robyns & Lawalrée (Hilliard, 2006)
	= *T. deceptum* N.E.Br	= *T. rhodesiacum* Pilg. (Hilliard, 2006)
	= *T. macrogyne* A.W.Hill	= *T. rogersii* A.W.Hill (Hilliard, 2006)
	= *T. nigrum* A.W.Hill	= *T. schweinfurthii* var. *laxum* Engl. (Baker and Hill, 1911)
	= *T. orientale* A.W.Hill	
2. *T. gracilarioides* A.W.Hill		
3. *T. gracile* A.W.Hill		= *T. palliolatum* A.W.Hill (Brown, 1932)
4. *T. gypsophiloides* A.W.Hill		
5. *T. infundibulare* N.Visser & M.M.le Roux		
6. *T. lobelioides* A.DC.		≡ *T. recurvifolium* Sond. (Hill, 1925)
7. *T. procerum* N.E.Br.		
8. *T. resedoides* A.W.Hill	= *T. junodii* A.W.Hill	= *T. burkei* A.W.Hill (Brown, 1932)
	= *T. mossii* N.E.Br	= *T. dumale* N.E.Br (Hilliard, 2006)
		≡ *T. welwitschii sensu* Baum *non* Hiern., name superfluous (Hill, 1910)
9. *T. vahrmeijeri* Brenan		