Phytotaxa 741 (1): 018–026
https://www.mapress.com/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.741.1.2

Phylogenetic analyses, morphological characteristics, and host specificity of a smut fungus on *Zonotriche* (Poaceae) from Tropical Africa reveal a new species, *Tilletia zonotriches* (Tilletiaceae)

TEODOR T. DENCHEV[1,2,5], CVETOMIR M. DENCHEV[1,2,6*], ANDRÉ FRAITURE[3,7] & MARTIN KEMLER[2,4,8]

[1]*Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin St., 1113 Sofia, Bulgaria*
[2]*IUCN SSC Rusts and Smuts Specialist Group, Sofia, Bulgaria*
[3]*Meise Botanic Garden, Domain of Bouchout, B-1860 Meise, Belgium*
[4]*Universität Hamburg, Institute of Plant Science and Microbiology, Organismic Botany and Mycology, Ohnhorststraße 18, 22609 Hamburg, Germany*
[5] *ttdenchev@gmail.com; https://orcid.org/0000-0002-7242-3307*
[6] *cmdenchev@yahoo.co.uk; https://orcid.org/0000-0001-6301-1629*
[7] *andre.fraiture@jardinbotaniquemeise.be; https://orcid.org/0000-0003-1440-1107*
[8] *martin.kemler@uni-hamburg.de; https://orcid.org/0000-0002-0738-4233*
**Corresponding author: cmdenchev@yahoo.co.uk*

Abstract

Tilletia species are highly specialized parasitic fungi on grasses. During examination of specimens of grasses in herbarium of the Meise Botanic Garden, Belgium, an ovariicolous smut fungus belonging to *Tilletia* was found on specimens of *Zonotriche decora* from the D.R. Congo and Zambia. These were the first finds of *Tilletia* specimens on *Zonotriche*. To clarify the taxonomic status of this species, we conducted a molecular study based on ITS and LSU rDNA sequences. The phylogenetic analyses indicate that this species differs from the *Tilletia* species with available molecular data. Additionally, this species possesses a distinctive morphological character, by which it can be easily distinguished from all species currently recognized in *Tilletia.* It produces by far the largest-sized spores in *Tilletia*, (45–)48–63(–68) µm long. Based on molecular and morphological evidence, and host specialization, a new species, *Tilletia zonotriches*, is described and illustrated. The phylogenetic placement and affinities of the new species in *Tilletia* are analyzed. *Tilletia zonotriches* differs from the only known smut fungus on *Zonotriche*, *Macalpinomyces zonotriches* on *Z. inamoena* from Zambia, by having significantly larger spores.

Key words: Democratic Republic of the Congo, new species, phylogeny, smut fungi, taxonomy, *Tilletia,* Zambia

Introduction

During examination of grass specimens in the herbarium of the Meise Botanic Garden, Belgium (BR; herbarium code according to Thiers 2025+), an ovariicolous smut fungus belonging to the genus *Tilletia* Tul. & C. Tul. was found on specimens of *Zonotriche* (C.E. Hubb.) J.B. Phipps from the Democratic Republic of the Congo and Zambia. This fungus was considered to represent an unknown species of *Tilletia*.

Zonotriche (Poaceae: Panicoideae) is a small genus in the tribe Tristachyideae, which contains 87 species in eight genera, specifically, *Danthoniopsis* Stapf, *Dilophotriche* (C.E. Hubb.) Jacq.-Fél., *Gilgiochloa* Pilg., *Loudetia* Hochst. ex Steud., *Loudetiopsis* Conert, *Trichopteryx* Nees, *Tristachya* Nees, and *Zonotriche* (Soreng *et al.* 2022). *Zonotriche* comprises three species (Soreng *et al.* 2017, 2022), with a geographic range restricted to Tropical Africa (Govaerts 2020).

Tilletia Tul. & C. Tul is a large, cosmopolitan genus in the Tilletiales, with 186 recognized species on host plants belonging to the grasses (Poaceae) (Bao *et al.* 2010, Vánky 2011a, b, Li *et al.* 2014, Denchev & Denchev 2018a, b, Denchev *et al.* 2018, McKenzie & Hallett 2022). Most commonly, their sori are produced in the ovaries, which are filled with a semi-agglutinated or powdery spore mass intermixed with sterile cells. In some species, the sori are formed on leaves and culms, as streaks. Exceptionally, the sori appear as swellings on the culms or cover the surface

 Accepted by Eric McKenzie: 23 Jan. 2026; published: 12 Feb. 2026

of the leaves, or form witches' brooms (Vánky 2013, Denchev & Denchev 2018a). None of the currently recognized species in *Tilletia* is known to infect plants in the tribe Tristachyideae.

The only smut fungus (Ustilaginomycotina) on *Zonotriche* is *Macalpinomyces zonotriches* Vánky on *Z. inamoena* (K. Schum.) Clayton from Zambia (Vánky 1996, 2011a, Vánky *et al.* 2011).

The aim of the present study was to clarify the taxonomic status of the *Tilletia* species on *Zonotriche decora* (Stapf) J.B. Phipps (Poaceae). A combined approach, using molecular data (based on ITS and LSU rDNA sequences), host specialization, and comparative morphology, revealed a new species, *T. zonotriches*, which is described and illustrated herein.

Material and methods

Materials

This study is based on phylogenetic and morphological analyses of three *Tilletia* specimens on *Zonotriche decora* from Tropical Africa.

DNA extraction, PCR amplification, and sequencing

For DNA extraction, sori of *Tilletia* were used. The sample was milled in the Bead Ruptor 12™ homogenizer (Omni International), using two steel beads. Genomic DNA was isolated using the my-Budget Plant DNA Kit™ (Bio-Budget Technologies GmbH, Germany), according to the manufacturer's protocol (protocol 1: "Isolation of DNA from plant material using lysis buffer SLS"). PCR using GoTaq™ Master Mix (Promega, U.S.A.) with the primer combinations M-ITS1/ITS4 (Stoll *et al.* 2003, White *et al.* 1990) and LR0R/NL4 (Moncalvo *et al.* 1995, O'Donnell 1992) was performed to amplify the ITS and LSU rDNA regions, which are the standard molecular markers for *Tilletia* (e.g., Li *et al.* 2014). Standard thermal cycling conditions with an annealing temperature of 53 °C were used for amplification. Five µl of PCR products were purified using a modified ExoSAP protokol (1 : 5 diluted in ddH_2O; New England Biolabs, USA). Amplicons were sequenced in both directions at Macrogen Europe (Macrogen Inc.) using the same primers as in the respective PCRs. Forward and reverse reads were checked for quality and assembled in Geneious 10.2.6 (Biomatters Ltd, New Zealand). Molecular work was conducted at the Mycology Laboratory at the Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences. Sequences were deposited in the NCBI nucleotide database (see Table 1 for accession numbers).

Phylogenetic analysis

The newly generated sequences of *Tilletia zonotriches* and representative sequences downloaded from GenBank (Table 1) were aligned in MAFFT using the online server version (Katoh *et al.* 2019). The ITS dataset was aligned with the e-ins-i option, the LSU dataset aligned under the l-ins-i option. Leading and trailing gaps of each alignment were coded as N. Subsequently, both alignments were concatenated and the best nucleotide substitution model was determined using ModelTest-NG (Darriba *et al.* 2020) implemented in raxmlGUI 2.0 (Edler *et al.* 2021). RaxML-NG (Kozlov *et al.* 2019), also implemented in raxmlGUI, was used for inferring a maximum likelihood phylogeny with 1000 thorough bootstrap replicates. iTOL 5 (Letunic & Bork 2021) was used for visualization of the phylogeny.

Morphological examination

Dried specimens of *Tilletia* were examined under a light microscope (LM) and a scanning electron microscope (SEM). For LM observations and measurements, spores and sterile cells were mounted in lactoglycerol solution (w : la : gl = 1 : 1 : 2) on glass slides, gently heated to boiling point to rehydrate the spores and sterile cells, and then cooled. The measurements of spores are given as min–max (extreme values) (mean ± 1 standard deviation). For SEM, spores and sterile cells were attached to a specimen stub by double-sided adhesive tape and coated with platinum in an ion sputter. The surface structure of spores and sterile cells was observed and photographed at 10 kV accelerating voltage using a JEOL JSM-7100F scanning electron microscope (Meise Botanic Garden, Belgium). The description below is based entirely on the specimens examined. The shapes of sterile cells and spores are arranged in descending order of frequency.

TABLE 1. Specimens and NCBI nucleotide database accession numbers used for phylogenetic analysis (newly generated sequences indicated in boldface).

Species	Host	Voucher	ITS	LSU	References
T. barclayana	*Paspalum distichum*	strain 832/WSP 68658	AF310168	AY818970	Levy *et al.* 2001 (ITS), Castlebury *et al.* 2005 (LSU)
T. boutelouae	*Bouteloua gracilis*	WSP 68661	NA	AY818973	Castlebury *et al.* 2005
T. cape-yorkensis	*Whiteochloa airoides*	BRIP 27011	MH231778	MH231778	Jayawardena *et al.* 2019
T. chionachnes	*Chionachne cyathopoda*	BRIP 26898	MH231779	MH231779	Jayawardena *et al.* 2019
T. eragrostiellae	*Eragrostiella bifaria*	BRIP: HUV 15805	MH231782	NA	Jayawardena *et al.* 2019
T. filisora	*Cenchrus polystachios*	BRIP 47729	MH231784	MH231784	Jayawardena *et al.* 2019
T. geeringii	*Eriachne festucacea*	BRIP 51851	KF055226	NA	Li *et al.* 2014
T. gigacellularis	*Bouteloua repens*	BRIP: HUV 20555	MH231785	MH231785	Jayawardena *et al.* 2019
T. imbecillis	*Oplismenus hirtellus*	BRIP 7831	MH231787	MH231787	Jayawardena *et al.* 2019
T. iowensis	*Phragmites communis*	BPI 863664	NA	AY818988	Castlebury *et al.* 2005
T. ischaemi	*Ischaemum rugosum*	BRIP: HUV 17453	MH231788	MH231788	Jayawardena *et al.* 2019
T. ixophori	*Anthoxanthum odoratum*	WSP 71170	NA	AY819010	Castlebury *et al.* 2005
T. kimberleyensis	*Chionachne cyathopoda*	BRIP 51857	MH231789	MH231789	Jayawardena *et al.* 2019
T. lageniformis	*Hyparrhenia rufa*	BRIP 47749	MH231791	MH231791	Jayawardena *et al.* 2019
T. lineata	*Arundinella nepalensis*	BRIP 26844	MH231793	MH231793	Jayawardena *et al.* 2019
T. mactaggartii	*Eriachne burkittii*	BRIP 51853	KF055227	KF055228	Li *et al.* 2014
T. majuscula	*Panicum majusculum*	BRIP 51841	MH231794	MH231794	Jayawardena *et al.* 2019
T. marjaniae	*Eriachne pulchella*	BRIP 49721	KF055224	KF055225	Li *et al.* 2014
T. micrairae	*Micraira dunlopii*	BRIP 52433	FJ862995	NA	Barrett *et al.* 2009
T. moliniae	*Phragmites australis*	TNS F-91252	LC603335	LC603335	Tanaka 2021
T. opaca	*Spinifex longifolius*	BRIP 27896	MH231798	MH231798	Jayawardena *et al.* 2019
T. panici-humilis	*Panicum humile*	BRIP: HUV 205832	MH231799	NA	Jayawardena *et al.* 2019
T. pseudochaetochloae	*Pseudochaetochloa australiensis*	BRIP 46730	MH231800	MH231800	Jayawardena *et al.* 2019
T. pseudoraphidis	*Pseudoraphis spinescens*	BRIP 51873	MH231801	MH231801	Jayawardena *et al.* 2019
T. pulcherrima	*Panicum virgatum*	WSP 71501	EU915293	NA	Carris *et al.* 2008
T. rugispora	*Paspalum plicatulum*	BRIP 47127/BRIP: HUV 19147	MH231803	AY818983	Jayawardena *et al.* 2019 (ITS), Castlebury *et al.* 2005 (LSU)
T. savilei	*Tripogon jacquemontii*	strain S097/V 859	AF399885	AY819018	Zhang *et al.* unpubl. (ITS), Castlebury *et al.* 2005 (LSU)
T. sehimicola	*Sehima nervosum*	BRIP 51847	MH231804	MH231804	Jayawardena *et al.* 2019
T. setariae-parviflorae	*Setaria parviflora*	BRIP 47735	MH231805	NA	Jayawardena *et al.* 2019
T. setariae-pumilae	*Setaria pumila*	BRIP: HUV 21399	MH231806	NA	Jayawardena *et al.* 2019
T. shivasii	*Arundinella nepalensis*	BRIP 52525	MH231807	NA	Jayawardena *et al.* 2019
T. sporoboli	*Sporobolus festivus*	BRIP: HUV 1880	MH231808	NA	Jayawardena *et al.* 2019
T. sumatiae	*Coix lacryma-jobi*	BRIP: HUV 17529/V 933	MH231809	AY818987	Jayawardena *et al.* 2019 (ITS), Castlebury *et al.* 2005 (LSU)
T. thailandica	*Eragrostis tenella*	BRIP 48134	MH231810	MH231810	Jayawardena *et al.* 2019
T. trachypogonis	*Trachypogon secundus*	BRIP: HUV 19626	MH231812	MH231812	Jayawardena *et al.* 2019
T. whiteochloae	*Whiteochloa sp.*	BRIP 51838	MH231815	MH231815	Jayawardena *et al.* 2019
T. xerochloae	*Xerochloa imberbis*	BRIP 54437	MH231816	MH231816	Jayawardena *et al.* 2019
T. zonotriches	***Zonotriche decora***	**SOMF 31500**	**PX591080**	**PX591081**	**this study**

Results

Phylogenetic analysis

ModelTest-NG determined GTR+FO+I+G4m as the best substitution model for the dataset. The phylogenetic analysis inferred similar species relationships as previous studies, with little statistical support for the relationsships of larger clades. The *Tilletia* specimens on *Zonotriche decora* formed a sister taxon to a clade containing *T. imbecillis* and *T. filisora* (Fig. 1). However, again there was no statistical support for such a relationship.

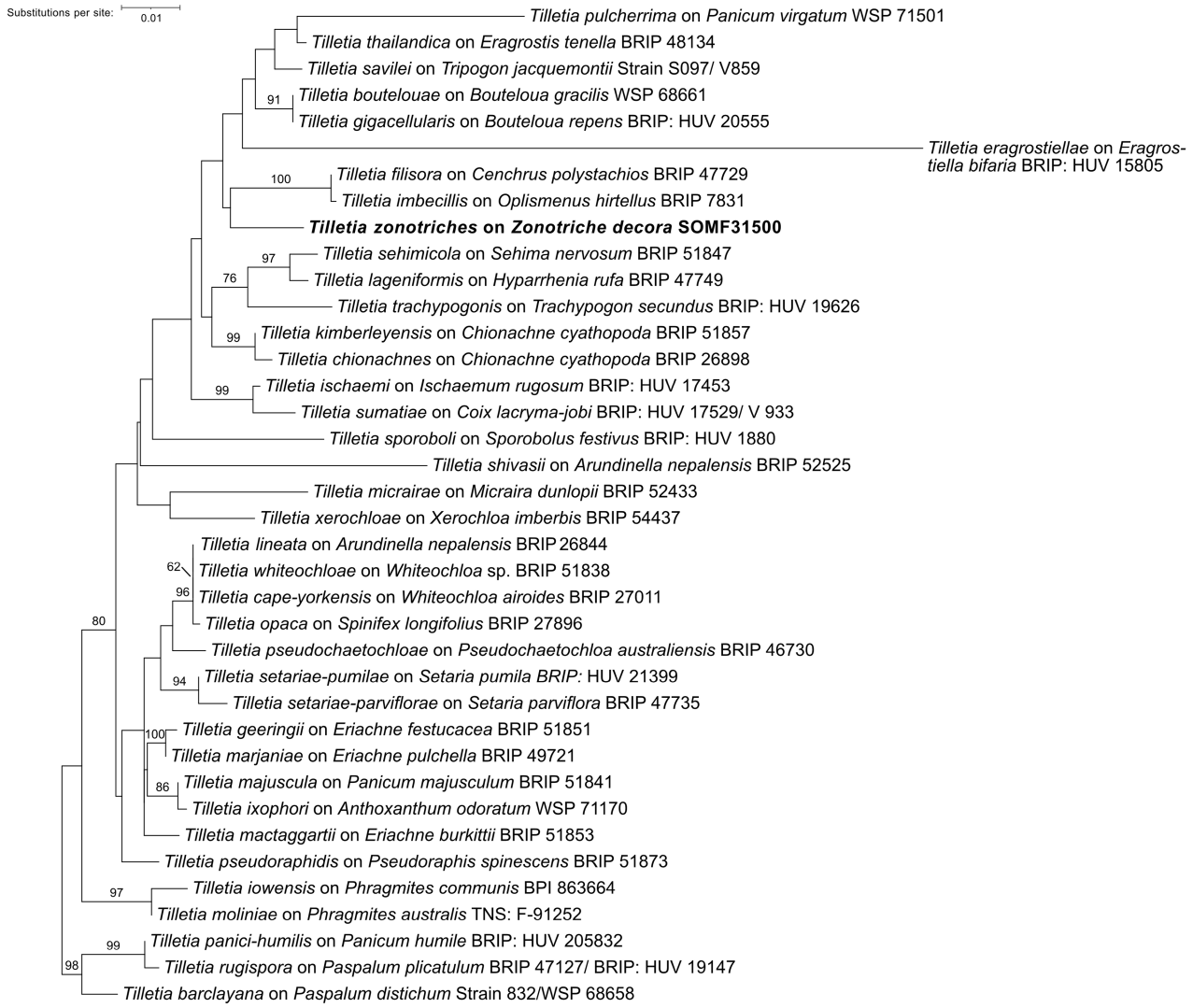


FIGURE 1. RAxML phylogeny of species in the genus *Tilletia* based on a MAFFT alignment of ITS and LSU rDNA sequences. Bootstrap values ≥ 60 are shown above branches. The phylogenetic tree was rooted with *Tilletia barclayana* (Bref.) Sacc. & P. Syd.*, T. panici-humilis* Pavgi & Thirum., and *T. rugispora* Ellis according to McTaggart & Shivas in Jayawardena *et al*. (2019).

Morphology

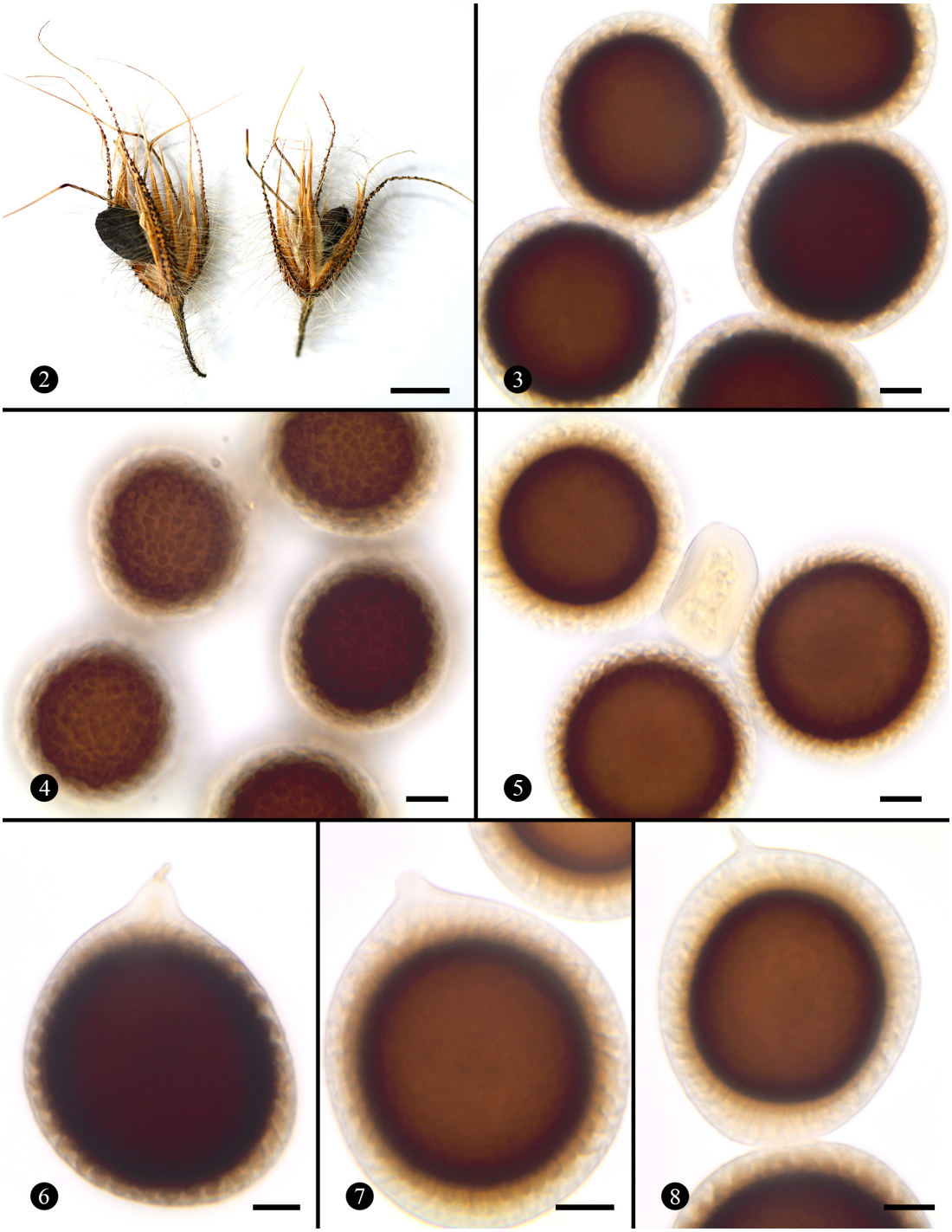
The morphological characteristics most commonly used for separating *Tilletia* species are: sorus location; length, wall thickness and ornamentation of sterile cells; spore shape and sizes, presence of a hyaline gelatinous sheath and its thickness; spore wall characteristics and ornamentation; presence and length of papilla and/or appendage. The morphological description of the studied smut fungus on *Zonotriche decora* was based on examination of specimens from the D.R. Congo and Zambia. Sori infect ovaries; sterile cells are usually collapsed and smaller than the spores, smooth, densely punctate or minutely verruculose; spores are subglobose, globose or broadly ellipsoidal, giant, (45–)48–63(–68) μm long, dark or very dark reddish brown, covered by 0.7–1.0 μm thick hyaline sheath; spore wall is irregularly thickened, (6.0–)7.5–10.5(–11.5) μm thick, with conical ornaments (covered by clusters of warts), 29–46

on equatorial circumference, in surface view appearing as irregular darker areas; spores are sometimes with a hyaline papilla, extending 3.7–8.0 µm beyond the ornamentation, or with narrow, hyaline appendage.

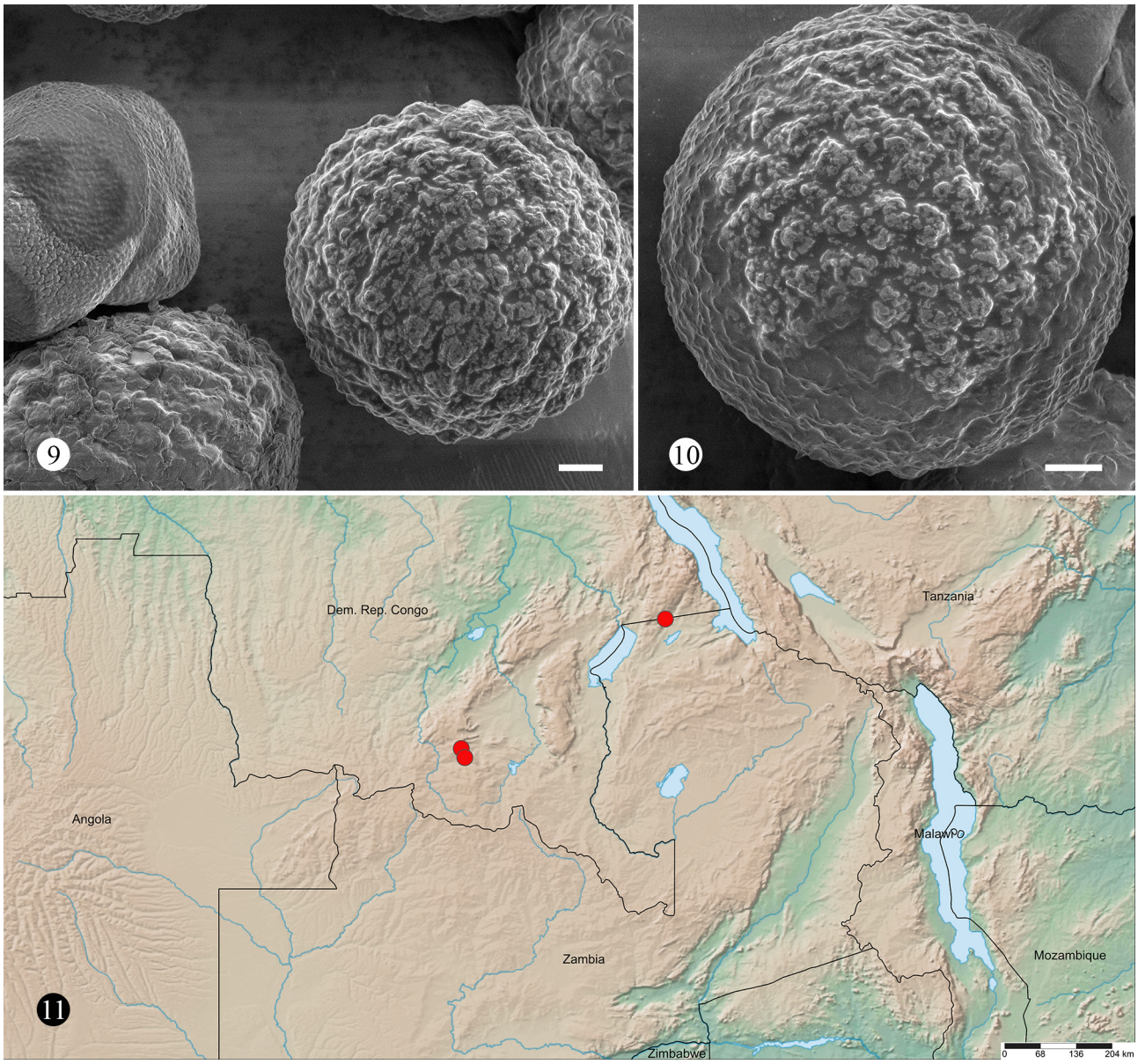
Taxonomy

It was found that the fungus on *Zonotriche decora* is specifically associated with the host. Based on the host specialization, phylogenetic data, and comparative morphology, we propose a new species of *Tilletia* on *Z. decora*.

Tilletia zonotriches T. Denchev, Denchev, Fraiture & Kemler, *sp. nov.* (Figs 2–10)
Index Fungorum number: IF 903997



FIGURES 2–8. *Tilletia zonotriches sp. nov.* on *Zonotriche decora* (from holotype). 2. Habit. 3, 4. Spores in LM (in median and surface view, respectively). 5. Spores (in median view) and a sterile cell in LM. Note the laminate wall of the sterile cell. 6–8. Spores in LM (in median view). Note the hyaline papillae in Figs 6, 7, and a hyaline appendage in Fig. 8. Scale bars: 2 = 0.5 cm, 3–8 = 10 µm.



FIGURES 9–11. *Tilletia zonotriches sp. nov.* on *Zonotriche decora*. 9. Spores and a sterile cell in SEM (from holotype). 10. Spore in SEM (from holotype). 11. Geographic distribution of *Tilletia zonotriches* (generated with Simple-Mappr, Shorthouse 2010). Scale bars: 9, 10 = 5 µm.

Holotype:—On *Zonotriche decora* (Stapf) J.B. Phipps (Poaceae). Democratic Republic of the Congo. Haut-Katanga Province: Kela, 11 April 1980, leg. F. Malaisse, no. 10555, fungus comm. & det. T.T. Denchev & C.M. Denchev (SOMF 31500).

ITS rDNA GenBank accession no.:—PX591080, **LSU rDNA** GenBank accession no.:—PX591081.

Diagnosis:—Differs from the other *Tilletia* species by specialization on *Zonotriche* and by having larger spores.

Etymology:—The epithet refers to the host genus, *Zonotriche*.

Description:—*Infection* local, only some spikelets of an inflorescence affected. *Sori* in single, strongly swollen ovaries, elongate to lemon-shaped, 7–10 × 1.5–3.5 mm, sometimes bearing rudimentary style and stigmas, easily visible between spreading floral bracts, covered by thick, yellowish brown to blackish brown pericarp that later ruptures irregularly, exposing powdery, blackish brown mass of spores and sterile cells. *Sterile cells* usually collapsed and smaller than the spores, variable in size, colour, and wall thickness, (16–)20–50(–56) µm long, hyaline to light yellowish brown; cell wall irregularly thickened, (1.6–)2.0–5.5(–7.5) µm thick, one-layered or laminate (Fig. 5). In SEM smooth, densely punctate (Fig. 9) or minutely verruculose. *Spores* subglobose, globose or broadly ellipsoidal, sometimes ovoid, (45–)48–63(–68) × (42–)45–58(–62) (55.3 ± 3.8 × 52.0 ± 3.3) µm (n_2 = 600), dark or very dark reddish brown, covered by 0.7–1.0 µm thick hyaline sheath; spore wall irregularly thickened, (6.0–)7.5–10.5(–11.5)

μm thick (including the (2.5–)3.2–6.5(–7.3) μm high ornamentation but excluding hyaline sheath), faint, 0.9–1.4(–1.7) μm thick inner layer may be observed in some lighter-coloured spores and in immature spores; ornaments conical, 29–46 on equatorial circumference, in surface view appearing as irregular darker areas; spores sometimes with a hyaline papilla (Figs 6, 7), extending 3.7–8.0 μm beyond the ornamentation, or with a narrow, hyaline appendage (Fig. 8); immature spores with hyaline to light yellowish brown colour, often similar to that of sterile cells. In SEM almost all spores covered by hyaline sheath, ornamentation composed of conical elements; in areas free of hyaline sheath, it becomes evident that the conical elements are covered by clusters of warts (Figs 9, 10).

Known host and distribution:—On *Zonotriche decora*, Africa (Democratic Republic of the Congo, Zambia) (Fig. 11).

Additional specimens examined:—On *Zonotriche decora*. Democratic Republic of the Congo. Haut-Katanga Province: 'Goma sud', 27 April 2006, leg. F. Malaisse *et al.*, no. MKS 226, fungus comm. & det. T.T. Denchev & C.M. Denchev (SOMF 31499). – Zambia. Northern Province, near Musosa, 25 May 1941, leg. H. Brédo, no. 4854, fungus comm. & det. T.T. Denchev & C.M. Denchev (SOMF 31501).

Comments:—For the first time, *Tilletia* infecting a species in *Zonotriche* is described. Additionally, *T. zonotriches* possesses a distinctive morphological character, by which it can be easily distinguished from all species currently recognized in *Tilletia.* It produces by far the largest-sized spores in *Tilletia*. The only other *Tilletia* that has spores exceeding 50 μm, is *T. eragrostiellae* Vánky *et al*. on *Eragrostiella bifaria* (Vahl) Bor from India, with spore length 40–60(–65) μm (Vánky 2011a). *Tilletia zonotriches* differs from the only known smut fungus on *Zonotriche*, *Macalpinomyces zonotriches* on *Z. inamoena*, by the presence of significantly larger spores (5–9 × 4–8 μm for *Macalpinomyces zonotriches*, Vánky 2011a).

Zonotriche decora is endemic to Tropical Africa, distributed in the D.R. Congo, Tanzania, Angola, and Zambia (Costa *et al.* 2004, Malaisse *et al.* 2016). The specimens of *Z. decora* from the D.R. Congo studied here were collected in copper steppe savannas in the Katangan Copperbelt. These plant communities are threatened by mining activities (Saad *et al.* 2012, Malaisse *et al.* 2016).

Acknowledgements

This study was supported by the Bulgarian National Science Fund (Grant no. KP-06-N51/10/16.11.2021). The visit of C.M. Denchev and T.T. Denchev to Herbarium of the Meise Botanic Garden (BR) received support from the SYNTHESYS Plus project (www.synthesys.info), which was financed by the H2020 Research Infrastructures Programme at the Botanic Garden Meise, Belgium (Grant no. BE-TAF-2445). T.T. Denchev and C.M. Denchev used facilities of the Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences upgraded in the frames of the project DiSSCo-BG (Upgrade of the Research Infrastructure 'Distributed System of Scientific Collections–Bulgaria') funded by the National Roadmap for Research Infrastructures, Ministry of Education and Science of the Republic of Bulgaria. The assistance of the staff of Herbarium of the Meise Botanic Garden is kindly acknowledged.

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