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## Redefining genera of cereal pathogens: *Oculimacula*, *Rhynchosporium* and *Spermospora*

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**Abstract:** The taxonomy of *Oculimacula*, *Rhynchosporium* and *Spermospora* is re-evaluated, along with that of phylogenetically related genera. Isolates are identified using comparisons of DNA sequences of the internal transcribed spacer ribosomal RNA locus (ITS), partial translation elongation factor 1-alpha (*tef1*), actin (*act*), DNA-directed RNA polymerase II largest (*rpb1*) and second largest subunit (*rpb2*) genes, and the nuclear ribosomal large subunit (LSU), combined with their morphological characteristics. *Oculimacula* is restricted to two species, *O. acuformis* and *O. yallundae*, with *O. aestiva* placed in *Cyphellophora*, and *O. anguioides* accommodated in a new genus, *Helgardiomycetes*. *Rhynchosporium s. str.* is restricted to species with 1-septate conidia and hooked apical beaks, while *Rhynchobrunnera* is introduced for species with 1–3-septate, straight conidia, lacking any apical beak. *Rhynchosporium graminicola* is proposed to replace the name *R. commune* applied to the barley scald pathogen based on nomenclatural priority. *Spermospora* is shown to be paraphyletic, representing *Spermospora* (type: *S. subulata*), with three new species, *S. arrhenatheri*, *S. loliiphila* and *S. zaeae*, and *Neospermospora gen. nov.* (type: *N. avenae*). *Ypsilina* (type: *Y. graminea*), is shown to be monophyletic, but appears to be of minor importance on cereals. Finally, *Vanderaaea gen. nov.* (type: *V. ammophilae*), is introduced as a new coelomycetous fungus occurring on dead leaves of *Ammophila arenaria*.

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## INTRODUCTION

Cereal crops are mainly cultivated for their edible grain. These crops are of enormous economic and social importance globally (McKevith 2004), but are susceptible to a wide array of foliar pathogens. Many of the most important cereal crop pathogens are fungi that cause leaf spot diseases (Dean *et al.* 2012, Doehlemann *et al.* 2017). These diseases inhibit grain filling by reducing photosynthesis and increasing plant respiration, leading to lower grain yields.

Several fungal genera pathogenic to cereals have recently been revised. These include *Cercospora* (grey leaf spot in maize, caused by *C. zeina*; Groenewald *et al.* 2013), *Exserohilum* (northern corn leaf blight of maize and sorghum caused by *E. turcicum*;

Hernández-Restrepo *et al.* 2018), *Pyrenophora* (tan spot of wheat caused by *P. tritici-repentis*, and net blotch of barley caused by *P. teres*; Marin-Felix *et al.* 2019a), *Pyricularia* rice blast caused by *Py. oryzae* (Klaubauf *et al.* 2014) and wheat blast caused by *Py. oryzae Triticum* pathotype (= *Py. graminis-tritici*), *Zymoseptoria* (*Septoria tritici* blotch caused by *Z. tritici*; Stukenbrock *et al.* 2012), *Parastagonospora* (*Septoria nodorum* blotch caused by *Pa. nodorum*; Quaadvlieg *et al.* 2013), *Bipolaris* (spot blotch caused by *B. sorokiniana*; Manamgoda *et al.* 2014), *Curvularia* (leaf spots on a range of grasses and cereals; Manamgoda *et al.* 2012), and *Ramularia* (*Ramularia* leaf spot of barley caused by *Ra. collo-cygni*; Videira *et al.* 2016), to name but a few.

Despite these numerous morphological studies coupled with DNA-based sequence analyses leading to taxonomic

revisions, the generic boundaries of many other foliar cereal pathogens remain insufficiently resolved. In many cases, existing pathogenic genera include a range of species that in the past were defined based only on their disease symptomatology, morphological similarity and/or host range. These genera are ripe for critical phylogenetic and morphological re-evaluation using modern methods. The aim of the present study was to re-circumscribe a complex of closely related fungal genera, namely *Rhynchosporium* (leaf blotch or scald of cereal and grass hosts), *Oculimacula* (eyespot disease of wheat), *Septogloeum* (leaf spots on strawberries, elms, mulberries and hazel), *Spermospora* (red leather leaf disease of oats) and *Ypsilina* (isolated from diverse substrates, including wheat).

## MATERIALS AND METHODS

### Isolates

Reference strains of the studied fungi are maintained in the following collections: the CBS culture collection (CBS) of the Westerdijk Fungal Biodiversity Institute (WI), Utrecht, the Netherlands, the Department of Plant Pathology, Institute of Integrative Biology, ETH, Zurich, Switzerland, Victorian Plant Pathogen Herbarium, VPRI, Bundoora, Australia, and the School of Life Sciences, University of Nottingham, UK. Colonies were sub-cultured on 2 % potato dextrose agar (PDA), oatmeal agar (OA), 2 % malt extract agar (MEA), and synthetic nutrient-poor agar (SNA), and incubated at 25 °C under continuous near-ultraviolet light to promote sporulation (for recipes see Crous *et al.* 2019b).

### DNA extraction, amplification (PCR) and phylogeny

Fungal mycelium (Table 1) was scraped from the agar surface of cultures with a sterile scalpel and the genomic DNA was isolated using the Wizard® Genomic DNA Purification Kit (Promega Corporation, WI, USA) following the manufacturers' protocols. Six loci were amplified following previously published protocols. First, the 28S nrRNA gene (LSU) and internal transcribed spacer regions with intervening 5.8S nrRNA gene (ITS) of the nrDNA operon were sequenced for all the isolates included in this study (for amplification conditions, see Fan *et al.* 2018). Amplification profiles of the partial DNA-directed RNA polymerase II second largest subunit gene (*rpb2*) and the partial translation elongation factor 1-alpha gene (*tef1*) followed Braun *et al.* (2018), while those of the partial actin gene (*act*) followed Videira *et al.* (2016) and of the partial DNA-directed RNA polymerase II largest subunit gene (*rpb1*) followed Pärtel *et al.* (2017). The resulting fragments were sequenced in both directions using the respective PCR primers and the BigDye Terminator Cycle Sequencing Kit v. 3.1 (Applied Biosystems Life Technologies, Carlsbad, CA, USA). DNA sequencing amplicons were purified through Sephadex G-50 Superfine columns (Sigma-Aldrich, St. Louis, MO) in MultiScreen HV plates (Millipore, Billerica, MA). Purified sequence reactions were analysed on an Applied Biosystems 3730xl DNA Analyzer (Life Technologies, Carlsbad, CA, USA). The DNA sequences were analysed and consensus sequences were computed using Geneious v. 11.1.5 (Kearse *et al.* 2012; <https://www.geneious.com>). The two Australian isolates of *Spermospora avenae* had a different extraction protocol, followed by Illumina sequencing (see Zaveri *et al.* 2020).

The sequences for each locus were subjected to megablast searches (Zhang *et al.* 2000) to identify similar sequences in the NCBI GenBank nucleotide database. Sequences of the individual loci (ITS, LSU, *act*, *tef1*, *rpb1*, *rpb2*) were aligned using MAFFT v. 7 (<http://mafft.cbrc.jp/alignment/server/index.html>, Katoh & Standley 2013), and the alignments were then manually edited in MEGA v. 7.0.21. Sequence Matrix v. 1.8 (<http://www.ggvaidya.com/taxondna/>) was used to concatenate the individual loci in various combinations. Phylogenetic trees were generated using Bayesian analyses (BA) (Supplementary Figs S1–S6, overview LSU phylogeny Fig. 1) performed with MrBayes v. 3.2.7 (Ronquist *et al.* 2012) as explained in Braun *et al.* (2018). The data matrices of different combinations of individual loci included: 1) all six loci containing all sequences from Figs S1–S6 (Fig. S7; ITS/LSU/*act*/*rpb1*/*rpb2*/*tef1*), 2) an alignment of the four loci which represent a more complete dataset (Fig. S8; ITS/LSU/*act*/*tef1*), 3) an alignment of the two loci for which the least number of sequences were available (Fig. S9; *rpb1*/*rpb2*) and 4) a reduced set of the 6-gene alignment derived from Fig. S7 (presented here as Fig. 2). Tree and character statistics for the different analyses are listed in Table 2. All resulting trees were printed with Geneious v. 11.1.5 and the layout of the trees was done in Adobe Illustrator v. CC 2017. Sequences derived in this study were deposited in GenBank (Table 1), the alignment in TreeBASE ([www.treebase.org](http://www.treebase.org); study number 27325), and taxonomic novelties in MycoBank ([www.MycoBank.org](http://www.MycoBank.org); Crous *et al.* 2004).

### Morphology

Slide preparations were mounted in lactic acid or Shear's mounting fluid, from colonies sporulating on SNA. Observations were made with a Nikon SMZ25 dissection-microscope, and with a Zeiss Axio Imager 2 light microscope using differential interference contrast (DIC) illumination and images recorded on a Nikon DS-Ri2 camera with associated software. Colony characters and pigment production were noted after 2–4 wk of growth on MEA, PDA and OA (Crous *et al.* 2019b) incubated at 25 °C.

## RESULTS

### Phylogeny

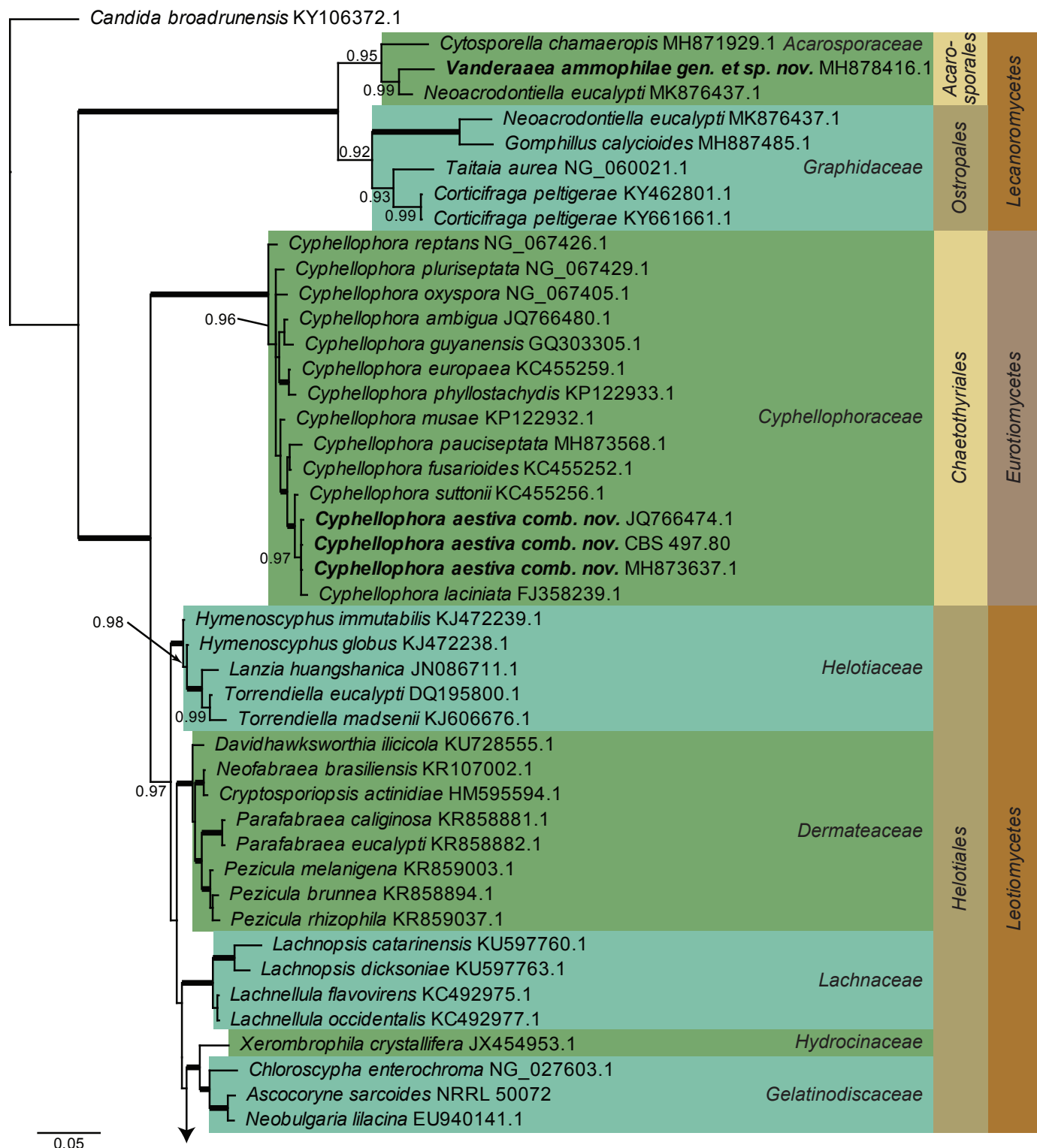
In the overview LSU phylogeny (Fig. 1, part 2), two cultures (CBS 497.80, CBS 886.68) were found to cluster outside of *Ploettnerulaceae* (*Helotiales*, *Leotiomycetes*). The ex-isotype culture (CBS 497.80) of *Pseudocercospora aestiva* clustered in *Cyphellophora* (*Cyphellophoraceae*, *Chaetothyriales*, *Eurotiomycetes*) and therefore a new combination in this genus is introduced for it below. A culture deposited in the CBS culture collection as *Spermospora avenae* (CBS 886.68) was found to be distantly related to *Neoacrodontiella eucalypti* (*Acarosporaceae*, *Acarosporales*, *Lecanoromycetes*) with no high similarity hits found in GenBank and therefore a new genus and species, *Vanderaaea ammophilae*, is introduced for it below.

Four-gene (Fig. S8) and 2-gene (Fig. S9) analyses were performed to confirm that the lack of *rpb1* and *rpb2* sequences for several samples is not influencing the tree topology in the 6-gene phylogenies (Figs 2, S7). The main difference in overall topology between the two 6-gene phylogenies (Figs 2, S7) is the placement of the *Helgardiomycetes* and *Ypsilina* clades, with the *Ypsilina* clade positioned in an unresolved basal polytomy in Fig.

S7 whereas it forms the most basal resolved lineage in Fig. 2. The 2-gene (Fig. S9) and 4-gene (Fig. S8) phylogenies resolved the same general lineages as the 6-gene phylogenies (Figs 2, S7) but differed mainly in the order of divergence of some clades. For example, *Spermospora* was consistently the sister lineage to *Oculimacula* whereas genera such as *Helgardiomycetes* and *Ypsilina* had alternative placements in the different tree

topologies. The 2-gene phylogeny (Fig. S9) is overall more similar to the 6-gene phylogenies (Figs 2, S7), with the exception of the placement of *Helgardiomycetes anguioides*.

Based on these phylogenetic trees, several taxonomic decisions were made and the phylogenetic relationships of individual groups are discussed under the Notes of respective taxa in the Taxonomy section below.



**Fig. 1.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the LSU sequence alignment. Bayesian posterior probabilities (PP) > 0.89 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Families, orders and classes are indicated with coloured blocks to the right of the tree. GenBank accession and/or culture collection numbers are indicated behind the species names. The tree was rooted to *Candida broadrunensis* (GenBank KY106372.1) and the taxonomic novelties described in this study are indicated in bold face.

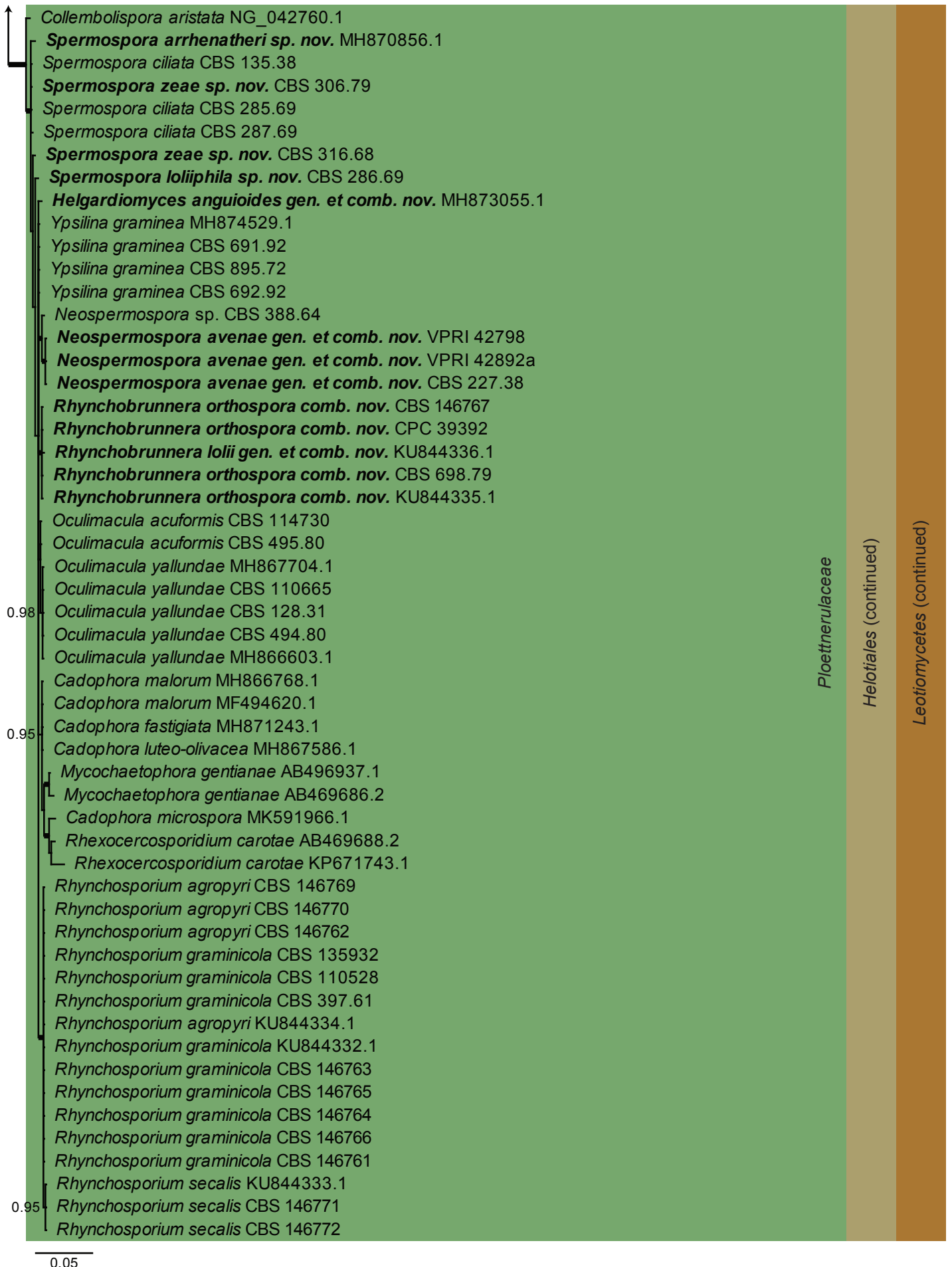
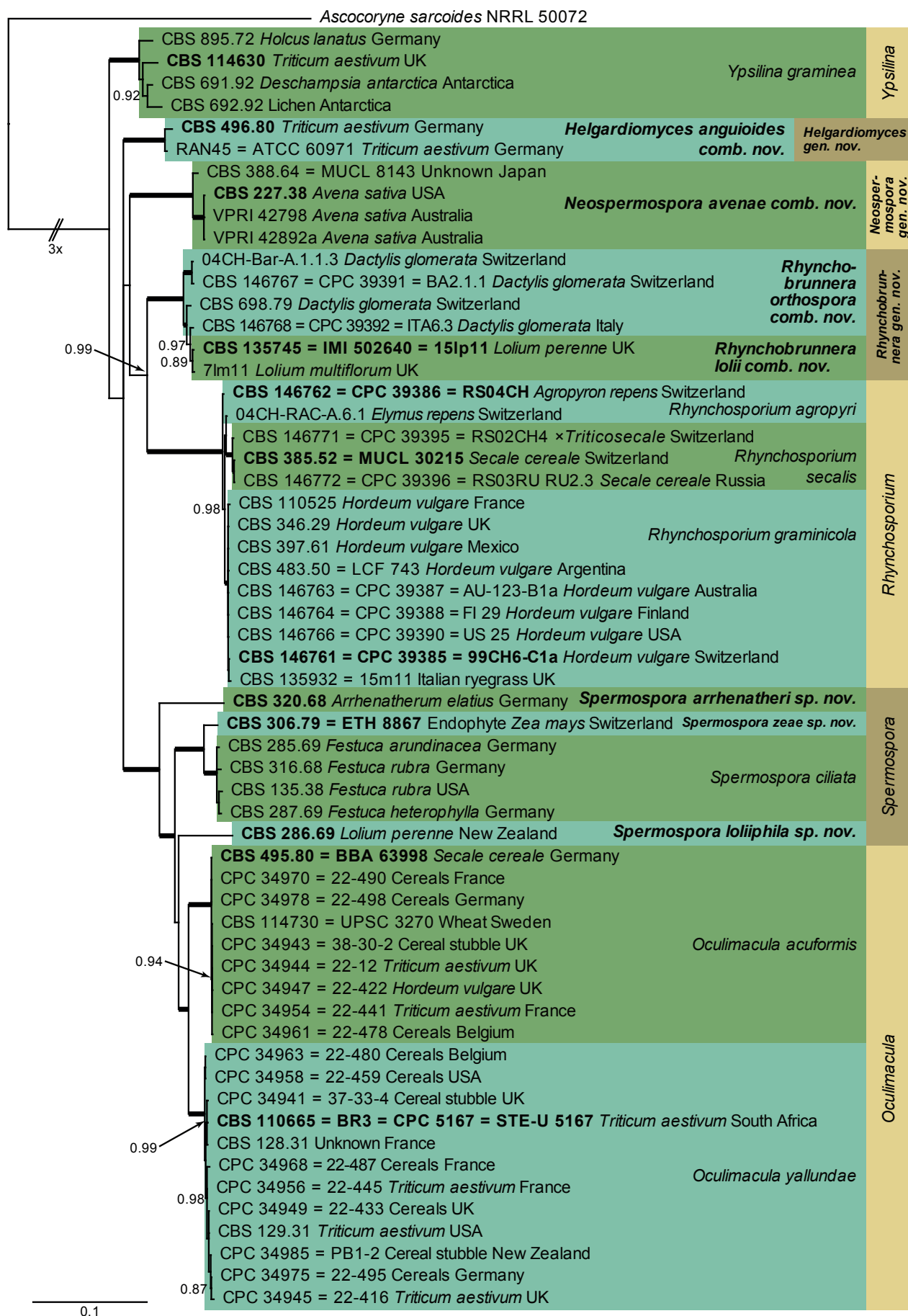


Fig. 1. (Continued).





**Fig. 2.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the reduced set 6-gene (ITS, LSU, *act*, *tef1*, *rpb1*, *rpb2*) sequence alignment. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and genera are indicated with coloured blocks to the right of the tree. Culture collection numbers are followed by the host and country of origin where known. The tree was rooted to *Ascocoryne sarcooides* (culture NRRL 50072) and the taxonomic novelties described in this study and cultures with a type status are indicated in bold face.

**Table 1.** Collection details, GenBank accession numbers and references of isolates and/or sequences considered in this study. Current species names are printed in bold and underlined text and the original or deposited names are listed per strain.

Current and original species names <sup>1</sup>	Substrate (including host); Country; Collection accession number(s) <sup>2</sup>	GenBank Accession number <sup>3</sup>						Sequence reference(s)	
		ITS	LSU	act	rpb1	rpb2	tef1		mtSSU <sup>4</sup> ; tub2 <sup>4</sup>
<b><u>Ascochyne sarcooides</u> (outgroup)</b>									
–	<i>Quercus robur</i> , dead branches; Netherlands; NRRL 50072	MycoCosm	MycoCosm	MycoCosm	MycoCosm	MycoCosm	MycoCosm	–; –	Gianoulis et al. (2014)
<b><u>Cyphellophora aestiva</u>, <b><u>comb. nov.</u></b></b>									
<i>C. vermispora</i>	<i>Hordeum vulgare</i> , root 4-wk-old in greenhouse; Germany; CBS 227.86	JQ766425.1	JQ766474.1	–	JQ766380.1	–	–	–; JQ766331.1	Feng et al. (2014)
<i>O. aestiva</i>	<i>Triticum aestivum</i> , stubble; Germany; CBS 497.80 = BBA 64002 <sup>ex-iso</sup> type of <i>Pseudocercospora aestiva</i>	MH861291.1	MW298373.1	MW297198.1	MW297302.1	–	–	–; MW297547.1	Vu et al. (2019); Present study
<b><u>Helgardiomycetes anguioides</u>, <b><u>gen. et comb. nov.</u></b></b>									
<i>H. anguioides</i>	<i>Triticum aestivum</i> , culm base; Germany; CBS 496.80 <sup>ex-iso</sup> type of <i>Pseudocercospora anguioides</i>	NR_158522.1	MH873055.1	MW297199.1	–	MW297368.1	LT990618.1	–; –	Marin-Felix et al. (2019b); Vu et al. (2019)
<i>H. anguioides</i>	<i>Triticum aestivum</i> ; Germany; RAN45 = ATCC 60971	AY266144.1	–	–	–	–	–	–; –	Stewart et al. (1999)
<b><u>Neospermospora avenae</u>, <b><u>gen. et comb. nov.</u></b></b>									
<i>Sp. avenae</i>	<i>Avena sativa</i> ; USA; CBS 227.38 <sup>ex-epi</sup> type of <i>Pseudodicosia avenae</i>	MW298276.1	MW298374.1	MW297200.1	–	MW297369.1	MW297456.1	MW298806.1; –	Present study
<i>Sp. avenae</i>	<i>Avena sativa</i> ; Australia; VPRI42798	MW298278.1	MW298376.1	–	MW297304.1	MW297371.1	MW297458.1	–; MT612938.1	Zaveri et al. (2020)
<i>Sp. avenae</i>	<i>Avena sativa</i> ; Australia; VPRI42892a	MW298279.1	MW298377.1	–	MW297305.1	MW297372.1	MW297459.1	–; MT612943.1	Zaveri et al. (2020)
<b><u>Neospermospora sp.</u></b>									
<i>Sp. avenae</i>	–; Japan; CBS 388.64 = MUCL 8143	MW298277.1	MW298375.1	MW297201.1	MW297303.1	MW297370.1	MW297457.1	–; –	Present study
<b><u>Oculimacula acufiformis</u></b>									
<i>O. aestiva</i>	<i>Triticum aestivum</i> ; Sweden; CBS 114730 = UPSC 3270	MG934454.1	MW298378.1	MW297202.1	MW297306.1	MW297373.1	MG934496.1	–; –	Marin-Felix et al. (2019b); Present study
<i>O. acufiformis</i>	<i>Secale cereale</i> , culm base; Germany; CBS 495.80 = BBA 63998 <sup>ex-iso</sup> type of <i>Pseudocercospora herpatrichoides</i> var. <i>acufiformis</i>	MH861289.1	MW298379.1	MW297203.1	MW297307.1	MW297374.1	MG934497.1	MW298807.1; –	Marin-Felix et al. (2019b); Vu et al. (2019); Present study
<i>T. acufiformis</i>	Cereal stubble; UK; CPC 34942 = 38-30-1	MW298280.1	MW298380.1	MW297204.1	MW297308.1	MW297375.1	MW297460.1	–; –	Present study
<i>T. acufiformis</i>	Cereal stubble; UK; CPC 34943 = 38-30-2	MW298281.1	MW298381.1	MW297205.1	MW297309.1	MW297376.1	MW297461.1	–; –	Present study
<i>T. acufiformis</i>	<i>Triticum aestivum</i> cv. Rapier; UK; CPC 34944 = 22-12	MW298282.1	MW298382.1	MW297206.1	MW297310.1	MW297377.1	MW297462.1	–; –	Present study
<i>T. acufiformis</i>	<i>Hordeum vulgare</i> ; UK; CPC 34947 = 22-422	MW298283.1	MW298383.1	MW297207.1	MW297311.1	MW297378.1	MW297463.1	–; –	Present study

Table 1. (Continued).

Current and original species names <sup>1</sup>	Substrate (including host); Country; Collection accession number(s) <sup>2</sup>	GenBank Accession number <sup>3</sup>							Sequence reference(s)
		ITS	LSU	act	rpb1	rpb2	tef1	mtSSU <sup>4</sup> ; tub2 <sup>4</sup>	
<i>T. aciformis</i>	<i>Triticum aestivum</i> ; UK; CPC 34953 = 22-440	MW298284.1	MW298384.1	MW297208.1	MW297312.1	MW297379.1	MW297464.1	MW298808.1; –	Present study
<i>T. aciformis</i>	<i>Triticum aestivum</i> ; France; CPC 34954 = 22-441	MW298285.1	MW298385.1	MW297209.1	MW297313.1	MW297380.1	MW297465.1	–; –	Present study
<i>T. aciformis/yallundae</i>	<i>Triticum aestivum</i> ; France; CPC 34955 = 22-444	MW298286.1	MW298386.1	MW297210.1	MW297314.1	MW297381.1	MW297466.1	MW298809.1; –	Present study
<i>T. aciformis/yallundae</i>	<i>Triticum aestivum</i> ; France; CPC 34957 = 22-446	MW298287.1	MW298387.1	MW297211.1	MW297315.1	MW297382.1	MW297467.1	–; –	Present study
<i>T. aciformis/yallundae</i>	Cereals; Belgium; CPC 34961 = 22-478	MW298288.1	MW298388.1	MW297212.1	MW297316.1	MW297383.1	MW297468.1	MW298810.1; –	Present study
<i>T. aciformis/yallundae</i>	Cereals; Belgium; CPC 34962 = 22-479	MW298289.1	MW298389.1	MW297213.1	MW297317.1	MW297384.1	MW297469.1	–; –	Present study
<i>T. aciformis</i>	Cereals; Belgium; CPC 34967 = 22-486	MW298290.1	MW298390.1	MW297214.1	MW297318.1	MW297385.1	MW297470.1	–; –	Present study
<i>T. aciformis</i>	Cereals; France; CPC 34969 = 22-488	MW298291.1	MW298391.1	MW297215.1	MW297319.1	MW297386.1	MW297471.1	–; –	Present study
<i>T. aciformis</i>	Cereals; France; CPC 34970 = 22-490	MW298292.1	MW298392.1	MW297216.1	MW297320.1	MW297387.1	MW297472.1	MW298811.1; –	Present study
<i>T. aciformis</i>	Cereals; France; CPC 34972 = 22-492	MW298293.1	MW298393.1	MW297217.1	MW297321.1	MW297388.1	MW297473.1	–; –	Present study
<i>T. aciformis</i>	Cereals; France; CPC 34973 = 22-493	MW298294.1	MW298394.1	MW297218.1	MW297322.1	MW297389.1	MW297474.1	–; –	Present study
<i>T. aciformis</i>	Cereals; Germany; CPC 34976 = 22-496	MW298295.1	MW298395.1	MW297219.1	MW297323.1	MW297390.1	MW297475.1	–; –	Present study
<i>T. aciformis</i>	Cereals; Germany; CPC 34977 = 22-497	MW298296.1	MW298396.1	MW297220.1	MW297324.1	MW297391.1	MW297476.1	MW298812.1; –	Present study
<i>T. aciformis</i>	Cereals; Germany; CPC 34978 = 22-498	MW298297.1	MW298397.1	MW297221.1	MW297325.1	MW297392.1	MW297477.1	–; –	Present study
<i>T. aciformis</i>	Cereals; Germany; CPC 34979 = 22-499	MW298298.1	MW298398.1	MW297222.1	MW297326.1	MW297393.1	MW297478.1	–; –	Present study
<i>O. aciformis</i>	<i>Secale cereale</i> ; Germany; RAC44 = ATCC 60973	AY266146.1	–	–	–	–	–	–; –	Stewart et al. (1999)
<i>H. aestiva</i>	<i>Triticum aestivum</i> ; USA: Washington; RAE22	AY266145.1	–	–	–	–	–	–; –	Stewart et al. (1999)
<i>O. yallundae</i>	<i>Triticum aestivum</i> ; USA: Washington; RH26 = Ph90-19-3	AY266169.1	–	–	–	–	–	–; –	Stewart et al. (1999)
<b><i>Oculimacula yallundae</i></b>									
<i>O. yallundae</i>	<i>Triticum aestivum</i> , stem base; Sweden; 141	KC989089.1	–	–	–	–	–	–; –	Grudzinska-Sterno et al. (2016)
<i>O. yallundae</i>	Cereals; UK; 22-432	AY713293.1	–	–	–	–	–	–; –	Karolewski et al. (2006)

Table 1. (Continued).

Current and original species names <sup>1</sup>	Substrate (including host); Country; Collection accession number(s) <sup>2</sup>	GenBank Accession number <sup>3</sup>						Sequence reference(s)	
		ITS	LSU	act	rpb1	rpb2	tef1		mtSSU <sup>4</sup> ; tub2 <sup>4</sup>
<i>O. yallundae</i>	Cereals; UK; 22-433	AY713294.1	–	–	–	–	–	–	Karolewski et al. (2006)
<i>O. yallundae</i>	<i>Triticum aestivum</i> ; South Africa; CBS 110665 = BR3 = CPC 5167 = STE-U 5167 <sup>exepitype of <i>Oculimacula yallundae</i></sup>	MG934456.1	MW298399.1	MW297223.1	–	MW297394.1	MG934498.1	MW298813.1; –	Marin-Felix et al. (2019b); Present study
<i>Ra. herpotrichoides</i>	<i>Triticum aestivum</i> , culm base; UK; CBS 118.47	–	MW298400.1	–	–	–	–	–	Present study
<i>O. yallundae</i>	–; France; CBS 128.31	MG934457.1	MW298401.1	MW297224.1	–	MW297395.1	MG934499.1	–	Marin-Felix et al. (2019b); Present study
<i>O. yallundae</i>	<i>Triticum aestivum</i> ; USA; CBS 129.31	MH855155.1	MH866603.1	MW297225.1	–	MW297396.1	–	–	Vu et al. (2019)
<i>O. yallundae</i>	<i>Hordeum vulgare</i> , culm base; Germany; CBS 494.80 = BBA 63987	JF412009.1	MW298402.1	–	–	–	MG934500.1	–	A. Tsang, unpublished; Marin-Felix et al. (2019b); Present study
<i>T. yallundae</i>	Cereal stubble; New Zealand; CPC 34939 = 11-3-18	MW298299.1	MW298403.1	MW297226.1	MW297327.1	MW297397.1	MW297479.1	–	Present study
<i>T. aciformis/yallundae</i>	Cereal stubble; UK; CPC 34940 = 37-27-7	MW298300.1	MW298404.1	–	MW297328.1	MW297398.1	MW297480.1	–	Present study
<i>T. aciformis/yallundae</i>	Cereal stubble; UK; CPC 34941 = 37-33-4	MW298301.1	MW298405.1	MW297227.1	MW297329.1	MW297399.1	MW297481.1	–	Present study
<i>T. yallundae</i>	<i>Triticum aestivum</i> ; UK; CPC 34945 = 22-416	MW298302.1	MW298406.1	MW297228.1	MW297330.1	MW297400.1	MW297482.1	–	Present study
<i>T. yallundae</i>	Cereals; UK; CPC 34946 = 22-417	MW298303.1	MW298407.1	MW297229.1	–	MW297401.1	MW297483.1	–	Present study
<i>T. yallundae</i>	Cereals; UK; CPC 34948 = 22-432	MW298304.1	MW298408.1	MW297230.1	MW297331.1	MW297402.1	MW297484.1	–	Present study
<i>T. yallundae</i>	Cereals; UK; CPC 34949 = 22-433	MW298305.1	MW298409.1	MW297231.1	–	MW297403.1	MW297485.1	–	Present study
<i>T. yallundae</i>	<i>Triticum aestivum</i> ; UK; CPC 34950 = 22-434	MW298306.1	MW298410.1	MW297232.1	MW297332.1	MW297404.1	MW297486.1	–	Present study
<i>T. yallundae</i>	<i>Triticum aestivum</i> ; UK; CPC 34951 = 22-435	MW298307.1	MW298411.1	–	–	–	–	–	Present study
<i>T. yallundae</i>	<i>Triticum aestivum</i> ; UK; CPC 34952 = 22-439	MW298308.1	MW298412.1	MW297233.1	–	MW297405.1	MW297487.1	–	Present study
<i>T. yallundae</i>	<i>Triticum aestivum</i> ; France; CPC 34956 = 22-445	MW298309.1	MW298413.1	MW297234.1	MW297333.1	MW297406.1	MW297488.1	MW298814.1; –	Present study
<i>T. yallundae</i>	Cereals; USA; Washington; CPC 34958 = 22-459	MW298310.1	MW298414.1	MW297235.1	MW297334.1	MW297407.1	MW297489.1	MW298815.1; –	Present study
<i>T. yallundae</i>	Cereals; USA; Washington; CPC 34959 = 22-460	MW298311.1	MW298415.1	MW297236.1	MW297335.1	MW297408.1	MW297490.1	–	Present study
<i>T. yallundae</i>	Cereals; Belgium; CPC 34963 = 22-480	MW298312.1	MW298416.1	MW297237.1	MW297336.1	MW297409.1	MW297491.1	–	Present study



Table 1. (Continued).

Current and original species names <sup>1</sup>	Substrate (including host); Country; Collection accession number(s) <sup>2</sup>	GenBank Accession number <sup>3</sup>							Sequence reference(s)
		ITS	LSU	act	rpb1	rpb2	tef1	mtSSU <sup>4</sup> ; tub2 <sup>4</sup>	
<i>T. yallundae</i>	Cereals; Belgium; CPC 34964 = 22-481	MW298313.1	MW298417.1	MW297238.1	MW297337.1	MW297410.1	MW297492.1	-; -	Present study
<i>T. yallundae</i>	Cereals; Belgium; CPC 34965 = 22-482	MW298314.1	MW298418.1	MW297239.1	MW297338.1	MW297411.1	MW297493.1	-; -	Present study
<i>T. yallundae</i>	Cereals; Belgium; CPC 34966 = 22-483	MW298315.1	MW298419.1	MW297240.1	-	MW297412.1	MW297494.1	-; -	Present study
<i>T. aciformis/yallundae</i>	Cereals; France; CPC 34968 = 22-487	MW298316.1	MW298420.1	MW297241.1	MW297339.1	MW297413.1	MW297495.1	MW298816.1; -	Present study
<i>T. yallundae</i>	Cereals; France; CPC 34971 = 22-491	MW298317.1	MW298421.1	MW297242.1	-	MW297414.1	MW297496.1	-	Present study
<i>T. yallundae</i>	Cereals; France; CPC 34974 = 22-494	MW298318.1	MW298422.1	MW297243.1	-	MW297415.1	MW297497.1	-	Present study
<i>T. yallundae</i>	Cereals; Germany; CPC 34975 = 22-495	MW298319.1	MW298423.1	MW297244.1	MW297340.1	MW297416.1	MW297498.1	MW298817.1; -	Present study
<i>T. yallundae</i>	Cereals; Germany; CPC 34980 = 22-500	MW298320.1	MW298424.1	MW297245.1	MW297341.1	MW297417.1	MW297499.1	-	Present study
<i>T. aciformis/yallundae</i>	Cereals; Germany; CPC 34981 = 22-501	MW298321.1	-	MW297246.1	MW297342.1	MW297418.1	MW297500.1	-	Present study
<i>T. aciformis/yallundae</i>	Cereals; Germany; CPC 34982 = 22-502	MW298322.1	MW298425.1	MW297247.1	MW297343.1	MW297419.1	MW297501.1	MW298818.1; -	Present study
<i>T. aciformis/yallundae</i>	Cereals; Germany; CPC 34983 = 22-503	MW298323.1	MW298426.1	MW297248.1	MW297344.1	MW297420.1	MW297502.1	-; -	Present study
<i>T. aciformis/yallundae</i>	Cereal stubble; New Zealand; CPC 34984 = PB1-1	MW298324.1	MW298427.1	MW297249.1	-	MW297421.1	MW297503.1	-; -	Present study
<i>T. yallundae</i>	Cereal stubble; New Zealand; CPC 34985 = PB1-2	MW298325.1	MW298428.1	MW297250.1	MW297345.1	MW297422.1	MW297504.1	-; -	Present study
<i>T. aciformis/yallundae</i>	Cereal stubble; New Zealand; CPC 34986 = PB1-6	MW298326.1	MW298429.1	MW297251.1	-	MW297423.1	MW297505.1	-; -	Present study
<i>T. yallundae</i>	Cereal stubble; New Zealand; CPC 34987 = PB1-7	MW298327.1	MW298430.1	MW297252.1	-	MW297424.1	MW297506.1	-; -	Present study
<i>T. aciformis/yallundae</i>	Cereal stubble; New Zealand; CPC 34988 = PB2-1	MW298328.1	MW298431.1	MW297253.1	-	MW297425.1	MW297507.1	-; -	Present study
<i>T. yallundae</i>	Cereal stubble; New Zealand; CPC 34989 = PB2-2	MW298329.1	MW298432.1	MW297254.1	-	MW297426.1	MW297508.1	-; -	Present study
<i>T. yallundae</i>	Cereal stubble; New Zealand; CPC 34990 = PB2-6	-	-	-	-	MW297427.1	-	-; -	Present study
<i>T. aciformis/yallundae</i>	Cereal stubble; New Zealand; CPC 34991 = PB2-7	MW298330.1	MW298433.1	MW297255.1	MW297346.1	MW297428.1	MW297509.1	-; -	Present study
<i>T. aciformis/yallundae</i>	Cereal stubble; New Zealand; CPC 34992 = PB3-1	MW298331.1	MW298434.1	MW297256.1	MW297347.1	MW297429.1	MW297510.1	-; -	Present study

Table 1. (Continued).

Current and original species names <sup>1</sup>	Substrate (including host); Country; Collection accession number(s) <sup>2</sup>	GenBank Accession number <sup>3</sup>							Sequence reference(s)
		ITS	LSU	act	rpb1	rpb2	tef1	mtSSU <sup>4</sup> ; tub2 <sup>4</sup>	
<i>T. yallundae</i>	Cereal stubble; New Zealand; CPC 34993 = PB3-2	MW298332.1	MW298435.1	–	–	MW297430.1	MW297511.1	–; –	Present study
<i>T. yallundae</i>	Cereal stubble; New Zealand; CPC 34996 = PB3-7	MW298333.1	MW298436.1	MW297257.1	–	MW297431.1	MW297512.1	–; –	Present study
<i>T. acufiformis/yallundae</i>	Cereal stubble; New Zealand; CPC 34998 = PB4-1	MW298334.1	MW298437.1	MW297258.1	MW297348.1	MW297432.1	MW297513.1	–; –	Present study
<i>T. acufiformis/yallundae</i>	Cereal stubble; New Zealand; CPC 34999 = PB4-3	MW298335.1	MW298438.1	MW297259.1	–	MW297433.1	MW297514.1	–; –	Present study
<i>T. acufiformis/yallundae</i>	Cereal stubble; New Zealand; CPC 35000 = PB4-5	MW298336.1	MW298439.1	MW297260.1	MW297349.1	MW297434.1	MW297515.1	–; –	Present study
<i>T. yallundae</i>	Cereal stubble; New Zealand; CPC 35001 = PB4-6	MW298337.1	MW298440.1	MW297261.1	–	MW297435.1	MW297516.1	–; –	Present study
<i>T. acufiformis/yallundae</i>	Cereal stubble; New Zealand; CPC 35002 = PB4-7	MW298338.1	MW298441.1	MW297262.1	–	MW297436.1	MW297517.1	–; –	Present study
<i>T. yallundae</i>	Cereal stubble; New Zealand; CPC 35003 = PB4-8	MW298339.1	–	MW297263.1	–	MW297437.1	–	–; –	Present study
<i>T. yallundae</i>	Cereal stubble; New Zealand; CPC 35005 = PB5-2	MW298340.1	–	–	–	MW297438.1	MW297518.1	–; –	Present study
<i>T. acufiformis/yallundae</i>	Cereal stubble; New Zealand; CPC 35006 = PB5-3	MW298341.1	MW298442.1	MW297264.1	MW297350.1	MW297439.1	MW297519.1	MW298819.1; –	Present study
<i>T. yallundae</i>	Cereal stubble; New Zealand; CPC 35007 = PB5-4	MW298342.1	–	MW297265.1	MW297351.1	MW297440.1	MW297520.1	MW298820.1; –	Present study
<i>T. acufiformis/yallundae</i>	Cereal stubble; New Zealand /CPC 35008 = PB5-5	MW298343.1	MW298443.1	MW297266.1	–	MW297441.1	MW297521.1	–	Present study
<i>T. acufiformis/yallundae</i>	Cereal stubble; New Zealand; CPC 35009 = PB5-6	MW298344.1	MW298444.1	MW297267.1	–	MW297442.1	MW297522.1	–	Present study
<i>T. yallundae</i>	Cereal stubble; New Zealand; CPC 35010 = PB5-10	MW298345.1	–	–	–	–	–	–	Present study
<i>O. yallundae</i>	<i>Triticum durum</i> var. Karim, stem base; Tunisia; TN 400	KF961611.1	–	–	–	–	–	–; –	S. Gargouri et al., unpublished
<i>O. yallundae</i>	<i>Triticum durum</i> ; Tunisia; TN 401	KF977547.1	–	–	–	–	–	–; –	S. Gargouri, unpublished
<b><i>Rhynchobernera lolii</i>, gen. et comb. nov.</b>									
<i>Rh. lolii</i>	<i>Lolium perenne</i> ; UK; 13lp11	KC819283.1	–	–	–	–	–	–; KC819293.1	King et al. (2013)
<i>Rh. lolii</i>	<i>Lolium multiflorum</i> ; UK; 4lm11	KC819281.1	–	–	–	–	–	–; KC819291.1	King et al. (2013)
<i>Rh. lolii</i>	<i>Lolium multiflorum</i> ; UK; 7lm11	KC819282.1	–	–	–	–	–	–; KC819292.1	King et al. (2013)

Table 1. (Continued).

Current and original species names <sup>1</sup>	Substrate (including host); Country; Collection accession number(s) <sup>2</sup>	GenBank Accession number <sup>3</sup>						Sequence reference(s)	
		ITS	LSU	act	rpb1	rpb2	tef1		mtSSU <sup>4</sup> ; tub2 <sup>4</sup>
<i>Rh. lolii</i>	<i>Lolium perenne</i> , diseased leaves; UK; CBS 135745 = IMI 502640 = 15lp11 <sup>ex</sup> <small>type of <i>Rhynchosporium lolii</i></small>	KU844336.1	KU844336.1	MW297268.1	MW297352.1	KU844339.1	–	MW298821.1; – Present study	Penselin <i>et al.</i> (2016); Present study
<b><i>Rhynchosporium orthospora</i>, comb. nov.</b>									
<i>Rh. orthosporum</i>	<i>Dactylis glomerata</i> ; Switzerland; 04CH-Bar-A.1.1.3	KU844335.1	KU844335.1	–	–	–	–	–; –	Penselin <i>et al.</i> (2016)
<i>Rh. orthosporum</i>	<i>Dactylus glomerata</i> , naturally infected leaf; Switzerland; CBS 146767 = CPC 39391 = BA2.1.1 = RS04CH-Bär-A.2.1.1	HM627470.1	MW298445.1	MW297269.1	MW297353.1	MW297443.1	HM627454.1	–; HM627429.1	Zaffarano <i>et al.</i> (2008)
<i>Rh. orthosporum</i>	<i>Dactylus glomerata</i> , naturally infected leaf; Italy; CBS 146768 = CPC 39392 = ITA6.3 = RS04ITA-D-6.3	HM627471.1	MW298446.1	MW297270.1	–	MW297444.1	HM627456.1	–; HM627431.1	Zaffarano <i>et al.</i> (2008)
<i>Rh. orthosporum</i>	<i>Dactylis glomerata</i> ; Switzerland; CBS 698.79	AY140669.1	MW298447.1	MW297271.1	MW297354.1	MW297445.1	–	–; –	Lee <i>et al.</i> (2001); Present study
<i>Rh. orthosporum</i>	<i>Dactylus glomerata</i> , naturally infected leaf; Italy; ITA2.2	HM627469.1	–	–	–	–	HM627455.1	–; HM627431.1	Zaffarano <i>et al.</i> (2008)
<b><i>Rhynchosporium agropyri</i></b>									
<i>Rh. agropyri</i>	<i>Elymus repens</i> ; Switzerland; 04CH-RAC-A.6.1	KU844334.1	KU844334.1	Ensembl	Ensembl	Ensembl	Ensembl	–; –	Penselin <i>et al.</i> (2016)
<i>Rh. agropyri</i>	<i>Agropyron repens</i> ; Switzerland; CBS 146762 = CPC 39386 = RS04CH = RS04CH-Käferberg-4-1A4.1 <sup>ex</sup> <small>type of <i>Rhynchosporium agropyri</i></small>	MW298346.1	MW298448.1	MW297272.1	MW297355.1	–	MW297523.1	–; –	Present study
<i>Rh. agropyri</i>	<i>Agropyron repens</i> ; Switzerland; CBS 146769 = CPC 39393 = K4.5A1 = RS04CH-Käferberg-4-5A1	MW298347.1	MW298449.1	–	–	–	MW297524.1	–; –	Present study
<i>Rh. agropyri</i>	<i>Agropyron repens</i> , naturally infected leaf; Switzerland; CBS 146770 = CPC 39394 = Daen1.1.2 = RS05CH Dänikon1.1.2	HM627480.1	MW298450.1	–	–	–	HM627463.1	–; HM627444.1	Zaffarano <i>et al.</i> (2008)
<i>Rh. agropyri</i>	<i>Agropyron caninum</i> , naturally infected leaf; Switzerland; CH3.4a.3	HM627475.1	–	–	–	–	HM627463.1	–; HM627444.1	Zaffarano <i>et al.</i> (2008)
<i>Rh. agropyri</i>	<i>Agropyron repens</i> , naturally infected leaf; Switzerland; D7.2	HM627473.1	–	–	–	–	HM627463.1	–; HM627433.1	Zaffarano <i>et al.</i> (2008)
<i>Rh. agropyri</i>	<i>Agropyron repens</i> , naturally infected leaf; Switzerland; ETH_ZT_Myc2337	HM627479.1	–	–	–	–	HM627463.1	–; –	Zaffarano <i>et al.</i> (2008)
<i>Rh. agropyri</i>	<i>Agropyron repens</i> , naturally infected leaf; Switzerland; K2B.4A1.1	HM627474.1	–	–	–	–	HM627463.1	–; HM627445.1	Zaffarano <i>et al.</i> (2008)

Table 1. (Continued).

Current and original species names <sup>1</sup>	Substrate (including host); Country; Collection accession number(s) <sup>2</sup>	GenBank Accession number <sup>3</sup>					Sequence reference(s)		
		ITS	LSU	act	rpb1	rpb2			
<i>Rh. agropyri</i>	<i>Agropyron repens</i> , naturally infected leaf; Switzerland; R2.A9.1	HM627476.1	–	–	–	–	HM627463.1	–; HM627445.1	Zaffarano et al. (2008)
<i>Rh. agropyri</i>	<i>Agropyron repens</i> , naturally infected leaf; Switzerland; SA3.1.1.1	HM627477.1	–	–	–	–	HM627463.1	–; HM627444.1	Zaffarano et al. (2008)
<i>Rh. agropyri</i>	<i>Agropyron repens</i> , naturally infected leaf; Switzerland; SA3.2.1.1	HM627478.1	–	–	–	–	HM627463.1	–; HM627444.1	Zaffarano et al. (2008)
<b><i>Rhynchosporium graminicola</i></b>									
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , leaf lesion; Switzerland; 00CHA1b	HM627468.1	–	–	–	–	HM627453.1	–; HM627428.1	Zaffarano et al. (2008)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Switzerland; 00CHH1a	HM627468.1	–	–	–	–	HM627466.1	–; HM627428.1	Zaffarano et al. (2008)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Switzerland; 01CH6a	HM627487.1	–	–	–	–	HM627453.1	–; HM627428.1	Zaffarano et al. (2008)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Switzerland; 99CH5A7a	HM627468.1	–	–	–	–	HM627460.1	–; HM627428.1	Zaffarano et al. (2008)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Switzerland; 99CH5E4a	HM627490.1	–	–	–	–	HM627453.1	–; HM627452.1	Zaffarano et al. (2008)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Switzerland; 99CH5H10a	HM627489.1	–	–	–	–	HM627453.1	–; HM627452.1	Zaffarano et al. (2008)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Australia; AUS3A2a	HM627468.1	–	–	–	–	HM627462.1	–; HM627437.1	Zaffarano et al. (2008)
<i>Rh. commune</i>	Barley grass/ <i>Hordeum leporinum</i> , naturally infected leaf; Australia; AUS6R16a	HM627468.1	–	–	–	–	HM627457.1	–; HM627438.1	Zaffarano et al. (2008)
<i>Rh. commune</i>	Barley grass/ <i>Hordeum leporinum</i> , naturally infected leaf; Australia; AUS6R19a	HM627468.1	–	–	–	–	HM627458.1	–; HM627448.1	Zaffarano et al. (2008)
<i>Rh. commune</i>	Barley grass/ <i>Hordeum leporinum</i> , naturally infected leaf; Australia; AUS6XA1.a	HM627485.1	–	–	–	–	HM627453.1	–; HM627447.1	Zaffarano et al. (2008)
<i>Rh. secalis</i>	<i>Hordeum vulgare</i> cv. Pipkin; UK; CBS 110524	MW298348.1	MW298451.1	MW297273.1	–	–	MW297525.1	–; –	Present study
<i>Rh. secalis</i>	<i>Hordeum vulgare</i> cv. Maeva; France; CBS 110525	MW298349.1	MW298452.1	MW297274.1	–	–	MW297526.1	–; –	Present study
<i>Rh. secalis</i>	<i>Hordeum vulgare</i> cv. Kymppi; Finland; CBS 110526	MW298350.1	MW298453.1	MW297275.1	–	–	MW297527.1	–; –	Present study
<i>Rh. secalis</i>	<i>Hordeum vulgare</i> cv. Tyra; Norway; CBS 110527	–	MW298454.1	MW297276.1	–	–	–	–; –	Present study



Table 1. (Continued).

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		ITS	LSU	act	rpb1	rpb2	tef1	mtSSU <sup>4</sup> ; tub2 <sup>4</sup>		
<i>Rh. secalis</i>	<i>Hordeum vulgare</i> cv. CC II (a); USA: California; CBS 110528	MW298351.1	MW298455.1	MW297277.1	MW297356.1	-	-	MW298822.1; -	Present study	
<i>Rh. commune</i>	Italian ryegrass; leaves; UK; CBS 135932 = 15m11	MW298352.1	MW298456.1	MW297278.1	MW297357.1	-	-	MW297528.1	MW298823.1; -	Present study
<i>Rh. commune</i>	<i>Hordeum vulgare</i> ; Switzerland; CBS 146761 = CPC 39385 = 99CH6-C1a <sup>8k</sup> -epiphyte of <i>Romularia hordei</i>	MW298353.1	MW298457.1	MW297279.1	-	-	-	MW297529.1	-	Present study
<i>Rh. commune</i>	<i>Hordeum vulgare</i> ; Australia; CBS 146763 = CPC 39387 = AU 123 = B1a	MW298354.1	MW298458.1	MW297280.1	MW297358.1	-	-	MW297530.1	-	Present study
<i>Rh. commune</i>	<i>Hordeum vulgare</i> ; Finland; CBS 146764 = CPC 39388 = FI 29 = H23	MW298355.1	MW298459.1	MW297281.1	MW297359.1	-	-	MW297531.1	-	Present study
<i>Rh. commune</i>	<i>Hordeum vulgare</i> ; Norway; CBS 146765 = CPC 39389 = NO 62 = C3	MW298356.1	MW298460.1	MW297282.1	MW297360.1	-	-	MW297532.1	-	Present study
<i>Rh. commune</i>	<i>Hordeum vulgare</i> ; USA; CBS 146766 = CPC 39390 = US 25 = 91	MW298357.1	MW298461.1	-	MW297361.1	-	-	MW297533.1	-	Present study
<i>Rh. secalis</i>	-; CBS 345.29	MW298358.1	MW298462.1	MW297283.1	-	-	-	MW297534.1	-	Present study
<i>Rh. secalis</i>	<i>Hordeum vulgare</i> ; UK; CBS 346.29	MW298359.1	MW298463.1	MW297284.1	-	-	-	MW297535.1	-	Present study
<i>Rh. secalis</i>	<i>Hordeum vulgare</i> ; Switzerland; CBS 384.52	MH857091.1	MW298464.1	MW297285.1	-	-	-	MW297536.1	-	Vu et al. (2019); Present study
<i>Rh. secalis</i>	<i>Hordeum vulgare</i> ; Mexico; CBS 397.61	MW298360.1	MW298465.1	MW297286.1	MW297362.1	-	-	MW297537.1	-	Vu et al. (2019); Present study
<i>Rh. secalis</i>	<i>Hordeum vulgare</i> ; Argentina; CBS 483.50 = LCF 743	MH856714.1	MH868233.1	MW297287.1	MW297363.1	-	-	MW297538.1	MW298824.1; -	Vu et al. (2019)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Ethiopia; ET.A5.a2	HM627484.1	-	-	-	-	-	HM627464.1	-	Zaffarano et al. (2008)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Ethiopia; ET.T1.4b	HM627468.1	-	-	-	-	-	HM627459.1	-	Zaffarano et al. (2008)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Ethiopia; ET3B3	HM627491.1	-	-	-	-	-	HM627464.1	-	Zaffarano et al. (2008)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Finland; FF31	HM627488.1	-	-	-	-	-	HM627453.1	-	Zaffarano et al. (2008)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Finland; FRA782	HM627486.1	-	-	-	-	-	HM627453.1	-	Zaffarano et al. (2008)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Norway; NKG11	HM627468.1	-	-	-	-	-	HM627467.1	-	Zaffarano et al. (2008)
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; New Zealand; NZ.2C6a	HM627492.1	-	-	-	-	-	HM627453.1	-	Zaffarano et al. (2008)
<i>Rh. secalis</i>	<i>Hordeum</i> sp.; USA; R157	AF384679.1	-	-	-	-	-	-	-	Goodwin (2002)

Table 1. (Continued).

Current and original species names <sup>1</sup>	Substrate (including host); Country; Collection accession number(s) <sup>2</sup>	GenBank Accession number <sup>3</sup>						Sequence reference(s)		
		ITS	LSU	act	rpb1	rpb2	tef1		mtSSU <sup>4</sup> ; tub2 <sup>4</sup>	
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; USA; RS149	HM627481.1	–	–	–	–	HM627453.1	–; HM627428.1	Zaffarano et al. (2008)	
<i>Rh. commune</i>	<i>Hordeum vulgare</i> , naturally infected leaf; Norway; RSW19.1	HM627468.1	–	–	–	–	HM627465.1	–; HM627437.1	Zaffarano et al. (2008)	
<i>Rh. commune</i>	<i>Hordeum vulgare</i> ; UK; UK7	KU844332.1	KU844332.1	Ensembl	Ensembl	Ensembl	Ensembl	–; –	Penselin et al. (2016)	
<b><i>Rhynchosporium secalis</i></b>										
<i>Rh. secalis</i>	<i>Secale cereale</i> ; Switzerland; O2CH4-6a.1	KU844333.1	KU844333.1	Ensembl	Ensembl	Ensembl	Ensembl	–; –	Penselin et al. (2016)	
<i>Rh. secalis</i>	<i>Secalis cereale</i> , naturally infected leaf; Russia; O2RU22	HM627472.1	–	–	–	–	HM627461.1	–; HM627443.1	Zaffarano et al. (2008)	
<i>Rh. secalis</i>	<i>Secalis cereale</i> , naturally infected leaf; Switzerland; 99CH1A1a	HM627482.1	–	–	–	–	HM627461.1	–; HM627443.1	Zaffarano et al. (2008)	
<i>Rh. secalis</i>	<i>Secalis cereale</i> , naturally infected leaf; Switzerland; 99CH1D4a	HM627483.1	–	–	–	–	HM627461.1	–; HM627446.1	Zaffarano et al. (2008)	
<i>Rh. secalis</i>	× <i>Triticosecale</i> ; Switzerland; Russia; CBS 146771 = CPC 39395 = RS02CH4 = 2a.1	MW298361.1	MW298466.1	MW297288.1	–	–	MW297539.1	–; –	Present study	
<i>Rh. secalis</i>	<i>Secale cereale</i> , leaves; Russia; CBS 146772 = CPC 39396 = RUB2.3 = RS03RU RU2.3	MW298362.1	MW298467.1	MW297289.1	–	–	MW297540.1	–; –	Present study	
<i>Rh. secalis</i>	<i>Secale cereale</i> ; Switzerland; CBS 385.52 = MUC1.30215 <sup>ex-epitype of <i>Marssonia secalis</i></sup>	MW298363.1	MW298468.1	MW297290.1	–	–	MW297541.1	–; –	Present study	
<b><i>Spermospora arrhenatheri, sp. nov.</i></b>										
<i>Se. oxysporum</i>	<i>Arrhenatherum elatius</i> ; Germany; CBS 320.68 <sup>ex-type of <i>Paraspermospora arrhenatheri</i></sup>	MH859144.1	MH870856.1	MW297291.1	–	–	MW297446.1	–	MW298825.1; –	Vu et al. (2019)
<b><i>Spermospora ciliata</i></b>										
<i>Sp. subulata</i>	<i>Festuca rubra</i> ; USA; CBS 135.38 <sup>authentic strain of <i>Cercosporiella subulata</i></sup>	–	MW298469.1	MW297292.1	–	–	MW297447.1	MW297542.1	MW298826.1; –	Present study
<i>Sp. subulata</i>	<i>Festuca arundinacea</i> ; Germany; CBS 285.69	MW298364.1	MW298470.1	MW297293.1	MW297364.1	–	MW297448.1	MW297543.1	–; –	Present study
<i>Sp. subulata</i>	<i>Festuca heterophylla</i> ; Germany; CBS 287.69	MW298365.1	MW298471.1	MW297294.1	–	–	MW297449.1	–	–; –	Present study
<i>Sp. subulata</i>	<i>Festuca rubra</i> ; Germany; CBS 316.68	MW298366.1	MW298472.1	–	–	–	–	–	–; –	Present study
<b><i>Spermospora loliphila, sp. nov.</i></b>										
<i>Sp. subulata</i>	<i>Lolium perenne</i> ; New Zealand; CBS 286.69 <sup>ex-type of <i>Spermospora loliphila</i></sup>	MW298367.1	MW298473.1	MW297295.1	–	–	MW297450.1	–	–; –	Present study

Table 1. (Continued).

Current and original species names <sup>1</sup>	Substrate (including host), Country; Collection accession number(s) <sup>2</sup>	GenBank Accession number <sup>3</sup>					Sequence reference(s)		
		ITS	LSU	act	rbp1	rbp2		tef1	mtSSU <sup>4</sup> ; tub2 <sup>4</sup>
<b><i>Spermospora zeae</i>, sp. nov.</b>									
<i>Sp. ciliata</i>	Endophyte of <i>Zea mays</i> ; Switzerland; CBS 306.79 = ETH 8867 <sup>ex-type of <i>Spermospora zeae</i></sup>	MW298368.1	MW298474.1	MW297296.1	–	MW297451.1	–	–; –	Present study
<b><i>Vanderaaea ammophilae</i>, gen. et sp. nov.</b>									
<i>Sp. avenae</i>	<i>Ammophila arenaria</i> , dead blades and leaves; Netherlands; CBS 886.68	MW298369.1	MH878416.1	MW297297.1	–	–	–	–; –	Vu et al. (2019); Present study
<b><i>Ypsilina graminea</i></b>									
<i>V. graminea</i>	<i>Triticum aestivum</i> , root rhizosphere; UK; CBS 114630 <sup>ex-type of <i>Volucrispora graminea</i></sup>	NR_160217.1	MH874529.1	MW297298.1	MW297365.1	MW297452.1	MW297544.1	MW298827.1; –	Vu et al. (2019); Present study
<i>V. graminea</i>	<i>Deschampsia antarctica</i> , leaf; Antarctica; CBS 691.92	MW298370.1	MW298475.1	MW297299.1	–	MW297453.1	–	–; –	Present study
<i>V. graminea</i>	Lichen; Antarctica; CBS 692.92	MW298371.1	MW298476.1	MW297300.1	MW297366.1	MW297454.1	MW297545.1	MW298828.1; –	Present study
<i>V. graminea</i>	<i>Holcus lanatus</i> ; Germany; CBS 895.72	MW298372.1	MW298477.1	MW297301.1	MW297367.1	MW297455.1	MW297546.1	–; –	Present study
<i>Y. graminea</i>	River; Portugal; UMB-111.01	GQ411306.1	–	–	–	–	–	–; –	Seena et al. (2010)
<i>Y. graminea</i>	River; Portugal; UMB-354.07	GQ411305.1	–	–	–	–	–	–; –	Seena et al. (2010)

<sup>1</sup> C.: *Cyphellophora*; H.: *Helgardia*; O.: *Oculimaculata*; Ra.: *Ramulispora*; Se.: *Septogloeum*; Sp.: *Spermospora*; T.: *Tapesia*; V.: *Volucrispora*; Y.: *Ypsilina*.

<sup>2</sup> ATCC: American Type Culture Collection, Virginia, USA; BBA: Biologische Bundesanstalt für Land- und Forstwirtschaft, Berlin-DPC; Culture collection of Pedro Crous, housed at CBS; ahlem, Germany; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; ETH: Swiss Federal Institute of Technology Culture Collection, Zurich, Switzerland; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium; IMI: International Mycological Institute, Egham, Basingstoke, United Kingdom; NRRL: National Center for Agricultural Utilization Research, Peoria, Illinois, USA; STE-U: Department of Plant Pathology, University of Stellenbosch, South Africa; UMB: culture collection of the Centre of Molecular and Environmental Biology (CBMA), Department of Biology of the University of Minho, Braga, Portugal; UPSC: Uppsala University Culture Collection of Fungi, Botanical Museum University of Uppsala, Uppsala, Sweden; VPRI: Victorian Department of Primary Industries, Knoxfield, Australia.

<sup>3</sup> ITS: internal transcribed spacer regions and intervening 5.8S nrRNA gene; LSU: partial 28S nrRNA gene, large subunit; act: partial actin gene; rpb1: partial DNA-directed RNA polymerase II largest subunit; rpb2: partial DNA-directed RNA polymerase II second largest subunit; tef1: partial translation elongation factor 1-alpha gene. Ensembl: sequence was obtained from a EnsemblFungi genome; MycoCosm: sequence was obtained from a MycoCosm genome.

<sup>4</sup> These two loci are added for completeness and were not used in the phylogenetic analyses due to the small number of successful novel sequences.

**Table 2.** Substitution models and other statistics for the Bayesian analyses in this study.

Locus <sup>1</sup>	Number of ingroup sequences	Number of unique site patterns	Total number of alignment positions	Substitution mode(s)	Number of generations	Number of trees sampled
<i>Individual genes</i>						
ITS (Fig. S1)	161	141	528	SYM+I+G	13 565 000	2 034 752
LSU (Fig. S2)	114	64	749	GTR+I	2 155 000	323 252
<i>act</i> (Fig. S3)	107	223	637	HKY+I+G	3 015 000	452 252
<i>rpb1</i> (Fig. S4)	68	131	497	SYM+I	975 000	146 252
<i>rpb2</i> (Fig. S5)	92	225	804	GTR+G	710 000	106 502
<i>tef1</i> (Fig. S6)	134	256	441	GTR+I	1 550 000	232 502
<i>Combined analyses</i>						
Reduced ITS/LSU/ <i>act/rpb1/rpb2/tef1</i> (Fig. 2)	58	121/53/216/128/225/224	3 608	See above	875 000	131 252
ITS/LSU/ <i>act/rpb1/rpb2/tef1</i> (Fig. S7)	165	141/68/231/130/229/237	3 608	See above	22 485 000	337 278
ITS/LSU/ <i>act/tef1</i> (Fig. S8)	164	141/68/231/237	2 303	See above	5 360 000	80 402
<i>rpb1/rpb2</i> (Fig. S9)	101	134/228	1 308	See above	1 040 000	15 602
<i>Overview analysis</i>						
LSU (Fig. 1)	98	340	822	See above	1 455 000	21 828

<sup>1</sup> ITS: internal transcribed spacer regions and intervening 5.8S nrRNA gene; LSU: partial 28S nrRNA gene, large subunit; *act*: partial actin gene; *rpb1*: partial DNA-directed RNA polymerase II largest subunit; *rpb2*: partial DNA-directed RNA polymerase II second largest subunit; *tef1*: partial translation elongation factor 1-alpha gene.



## Taxonomy

***Cyphellophora aestiva*** (Nirenberg) Crous, **comb. nov.** MycoBank MB838071. Fig. 3.

**Basionym:** *Pseudocercospora aestiva* Nirenberg, *Z. PflKrankh. PflSchutz* **88**: 246. 1981.

**Synonyms:** *Ramulispora aestiva* (Nirenberg) E.L. Stewart & Crous, *Mycol. Res.* **103**: 1497. 1999.

*Helgardia aestiva* (Nirenberg) Crous & W. Gams, *Eur. J. Pl. Path.* **109**: 848. 2003.

*Oculimacula aestiva* (Nirenberg) Crous, *IMA Fungus* **5**: 103. 2014.  
*Cyphellophora vermispota* A. Walz & de Hoog, *Antonie van Leeuwenhoek* **53**: 143. 1987.

**Typus:** **Germany**, Oldenburg, on stubble of *Triticum aestivum*, 1979, *H. Nirenberg* (**holotype** B); culture ex-holotype BBA 64002 = CBS 497.80.

**Notes:** Species of *Cyphellophora* are characterised by having elongated, curved, one- to multiseptate conidia, and well-developed, flared phialides, which frequently develop directly on fungal hyphae (Crous *et al.* 2009). The genus includes some species which are reported from mild skin and nail infections of humans (de Hoog *et al.* 2000, Réblová *et al.* 2013), while others occur widespread in nature and have been isolated from soil, plants, water and other substrates (Feng *et al.* 2014, Crous *et al.* 2019a). The morphology of *Cyphellophora aestiva* (CBS 497.80 from *Triticum aestivum*, Germany) is identical to *C. vermispota* (CBS 227.86) described from *T. aestivum* stalks collected in Germany (ex-type culture CBS 228.86; Walz & de Hoog 1987). The ITS sequence of CBS 497.80 is identical (548/548 bp) to ITS sequence of the ex-type of *C. vermispota* (MUCL 43739 = CBS 228.86; GenBank NR\_121463) and it differed one nucleotide from the ITS sequence of *C. vermispota* culture CBS 227.86 (GenBank JQ766425); it is 617/624 (99 %, including two gaps) similar to the ITS sequence of the ex-type of *C. laciniata* (CBS 190.61; GenBank NR\_121335). The LSU sequence differs with a single nucleotide over 763 bp from CBS 227.86 (GenBank JQ766474) and with two indels over 889 bp from the ex-type of *C. vermispota* (CBS 228.86 = MUCL 43739; GenBank MH873637); it is 881/885 (99 %) similar to the LSU sequence of the ex-type of *C. laciniata* (CBS 190.61; GenBank FJ358239). The *tub2* sequence is identical (385/385 bp) to that of *C. vermispota* culture CBS 227.86 (GenBank JQ766331) and differs two nucleotides from the sequence of the ex-type of *C. vermispota* (368/370 bp, CBS 228.86 = MUCL 43739; GenBank JQ766332); it is 341/387 (88 %,

including four gaps) similar to the *tub2* sequence of the ex-type of *C. laciniata* (CBS 190.61; GenBank JQ766329).

***Helgardiomycetes*** Crous, **gen. nov.** MycoBank MB838072.

**Etymology:** *Helgardiomycetes*, composed of Helgard, named after the German mycologist and phytopathologist, Dr Helgard I. Nirenberg, who first recognized the distinctiveness of these fungi on cereals, and -myces (fungus).

**Mycelium** consisting of hyaline, smooth, septate, branched hyphae. **Conidiophores** mostly solitary to aggregated, rarely branched, hyaline, smooth, with terminal conidiogenous cells that have apical sympodial proliferation, and inconspicuous scars. **Conidia** long, flexuous, subcylindrical, hyaline, smooth, multiseptate, apex subobtuse, base truncate, hila unthickened.

**Type species:** *Helgardiomycetes anguioides* (Nirenberg) Crous

**Ex-type culture:** CBS 496.80.

***Helgardiomycetes anguioides*** (Nirenberg) Crous, **comb. nov.** MycoBank MB838073.

**Basionym:** *Pseudocercospora anguioides* Nirenberg, *Z. PflKrankh. PflSchutz* **88**: 246. 1981.

**Synonyms:** *Ramulispora herpotrichoides* var. *anguioides* (Nirenberg) U. Braun, *Nova Hedwigia* **56**(3–4): 433. 1993.

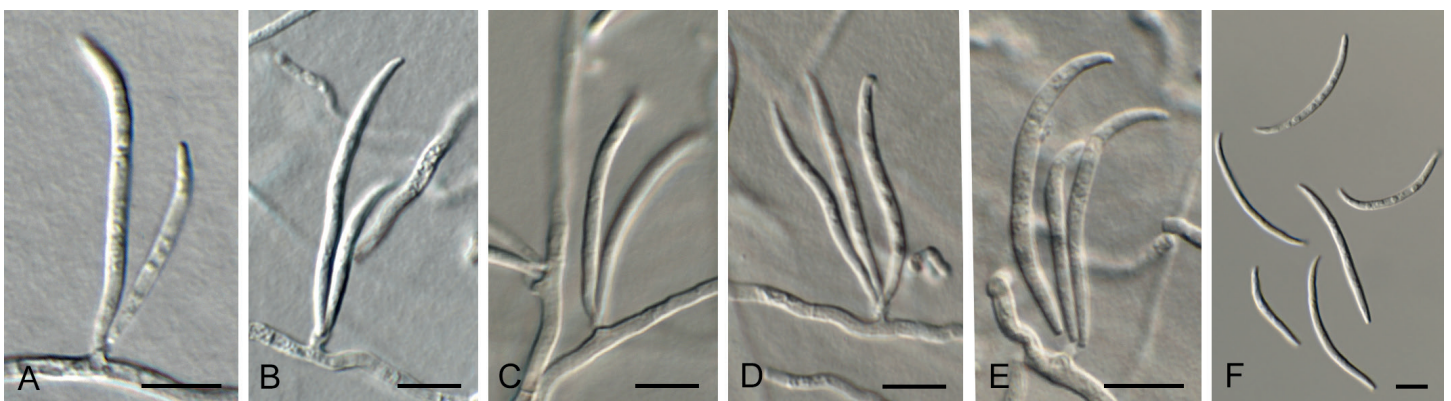
*Ramulispora anguioides* (Nirenberg) Crous, *S. Afr. J. Bot.* **61**: 47. 1995.

*Helgardia anguioides* (Nirenberg) Crous & W. Gams, *Eur. J. Pl. Path.* **109**: 846. 2003.

*Oculimacula anguioides* (Nirenberg) Crous, *IMA Fungus* **5**: 103. 2014.

**Typus:** **Germany**, Göttingen, culm base of *Triticum aestivum*, 1979, *H. Nirenberg* (**holotype** B); culture ex-holotype BBA 64003 = CBS 496.80.

**Notes:** Colonies differ from those of *Oculimacula* in that they are fast growing, and dull pinkish on PDA, velvety, with entire margin. Conidia are long and flexuous, up to 280 µm in length, and pluriseptate (Nirenberg 1981). In contrast to *Oculimacula*, *H. anguioides* is weakly aggressive to wheat (Bateman 1988). The species formed a fully or well-supported lineage in most analyses of the loci for which sequences were available (ITS, *act*, *rpb2*, *tef1*; Figs 2, S1, S3, S5, S6; multigene phylogenies Figs 2,



**Fig. 3.** *Cyphellophora aestiva* (CBS 497.80). **A–E.** Hyphae with phialides giving rise to clusters of conidia. **F.** Conidia. Scale bars = 10 µm.

S7–S9), with the exception of LSU where it was not well resolved (Figs 1, S2).

***Neospermospora*** Crous & U. Braun, **gen. nov.** MycoBank MB838074.

**Etymology:** Referring to its morphological similarity to *Spermospora*.

Phytopathogenic, causing leaf spots. *Mycelium* internal, hyaline to olivaceous, septate, branched, becoming swollen in epidermal cells, and at times aggregating into swollen, vesicular conidiogenous cells, hyaline to pale olivaceous, smooth. *Conidiogenous cells* form narrow, blunt or pointed penetration tubes that penetrate the outer epidermal cells, giving rise to a single, terminal conidium. *Conidia* narrowly fusoid with long narrow rostrum, septate, not constricted at septa, straight to curved, often with single filiform sub-basal appendage, hyaline, smooth, with obconically truncate base.

**Type species:** *Neospermospora avenae* (R. Sprague & Aar.G. Johnson) Crous & U. Braun

**Reference culture:** CBS 227.38.

***Neospermospora avenae*** (R. Sprague & Aar.G. Johnson) Crous & U. Braun, **comb. nov.** MycoBank MB838075. Fig. 4.

**Basionym:** *Pseudodiscosia avenae* R. Sprague & Aar.G. Johnson, *Mycologia* **28**(2): 183. 1936.

**Synonym:** *Spermospora avenae* (R. Sprague & Aar.G. Johnson) R. Sprague, *Diseases of Cereals and Grasses of North America*: 430. 1950.

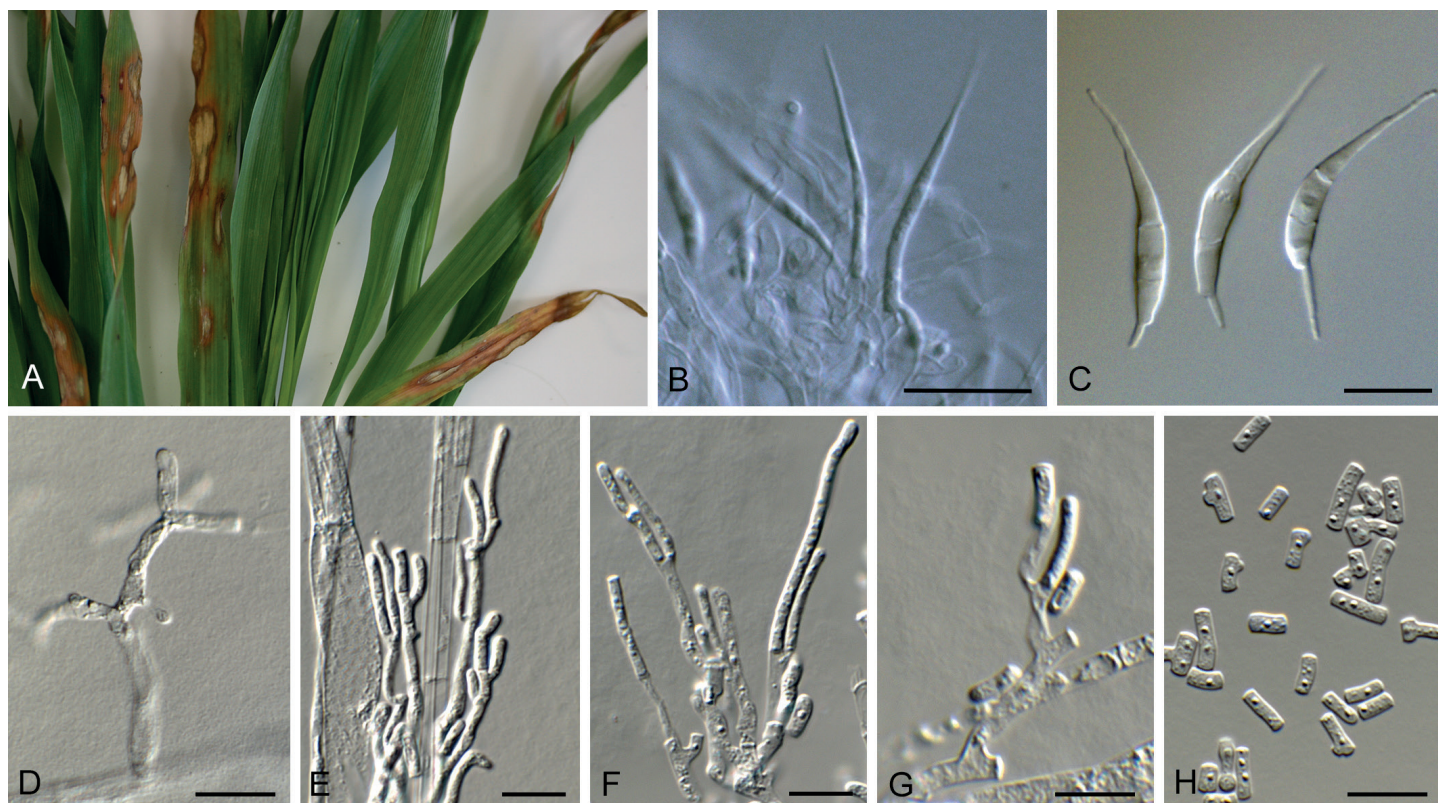
**Typus:** USA, Washington, Klichitat Co., High Prairie, on *Avena sativa*, 10 Feb. 1934, R. Sprague [**lectotype**, designated by Braun (1995: 238), K]; isoelectotypes BPI 407544, 407549, CINC-F0008022, ISC-F-0098103, K, MICH 5608, NY01087070, OSC 8036, RMS 0024665, WIS-F-0033535. USA, Oregon, near Corvallis, on *A. sativa*, Mar. 1938, R. Sprague (**epitype** designated here CBS 227.38, MBT394907, preserved as a metabolically inactive culture; culture ex-epitype CBS 227.38 – reference strain deposited by R. Sprague).

**Additional isolates examined:** Australia, Victoria, Maryborough, on leaves of *Avena sativa*, 8 Sep. 2014, P. Zwer, VPRI 42798; Victoria, Wal Wal, on leaves of *A. sativa*, J. Edwards, 3 Oct. 2016, VPRI 42892a. Japan, H. Kurata, No. 4320, MUCL 8143 = CBS 388.64.

**Description and illustration of characteristics in vivo:** Braun (1995: 238 and 239, fig. 220).

**Notes:** *Neospermospora avenae* causes red leather leaf disease of oats, reducing grain yield and hay quality, and has been reported from Europe, the USA, Turkey and Australia (Cunningham 1990, Zaveri *et al.* 2020). Based on the isolates included in the phylogeny, it appears that an undescribed species of *Neospermospora* (CBS 388.64) also occurs on *Avena* in Japan. This isolate is genetically slightly different from the other included cultures of *N. avenae* with the following number of substitutions compared to the other sequenced strains: three (and one indel) in ITS, seven in LSU, 10 in *act*, two in *rpb1*, 11 in *rpb2*, and 17 substitutions in *tef1*.

Cultures of *N. avenae* formed a microconidial synanamorph in culture with hyaline, aseptate conidia. The species formed a fully supported lineage in all analyses of different combinations of the



**Fig. 4.** *Neospermospora avenae*. **A–C** (VPRI 42798). Disease symptoms on *Avena sativa*. **B.** Conidiogenous cells giving rise to macroconidia. **C.** Macroconidia. **D–H** (CBS 227.38). Hyphae giving rise to a microconidial synsexual morph. Scale bars = 10 µm.



six loci studied here (Figs 1, 2, S1–S9). Sprague & Johnson (1936) failed to designate a holotype for *Pseudodiscosia avenae*. They only cited several “co-types” which required lectotypification (Braun 1995). That is followed here for designating an epitype obtained from a living culture that served as the source of the sequence data.

***Oculimacula*** Crous & W. Gams, *Eur. J. Pl. Path.* **109**: 845. 2003.  
*Synonym*: *Helgardia* Crous & W. Gams, *Eur. J. Pl. Path.* **109**: 845. 2003.

*Ascomata* 0.5–2.5 mm diam, apothecial, sessile, gregarious, circular to lobate, on a subiculum of white to dark brown hyphae, attached to substrate via a superficial mat of pale brown, thin hyphae. *Disk* smooth, grey with a pale grey margin, becoming emarginate and flattened to convex at maturity. *Receptacle* pale brown to grey-brown, cup-shaped. *Medullary excipulum* of multiseptate, hyaline hyphae. *Ectal excipulum* of thin-walled, dark brown, angular cells, becoming more elongated towards margin. *Paraphyses* filiform with obtuse ends, similar in length to asci. *Asci* 8-spored, unitunicate, clavate to subcylindrical or fusoid, with a short stalk, and an apical pore staining blue in Melzer’s reagent. *Ascospores* bi- to multiseriate, hyaline, smooth, aseptate, fusoid to subcylindrical or clavate with rounded ends, mostly straight. *Conidiophores* fasciculate or solitary on superficial mycelium, or arising from pale brown stromata, subcylindrical to geniculate-sinuuous, rarely branching, hyaline to pale olivaceous, smooth, consisting of conidiogenous cells only, or slightly differentiated with up to 2 septa. *Conidiogenous cells* integrated, proliferating sympodially at apex, with inconspicuous, dense geniculations; *conidiogenous loci* unthickened, inconspicuous, not darkened. *Conidia* solitary, hyaline, smooth, arranged in slimy packets, acicular, filiform, straight to curved, one- to multiseptate, forming smaller, secondary conidia via microcyclic conidiation (Marin-Felix *et al.* 2019a).

*Type species*: *Oculimacula yallundae* (Wallwork & Spooner) Crous & W. Gams

*Ex-type culture*: CBS 110665.

***Oculimacula acuformis*** (Nirenberg) Y. Marín & Crous, *Stud. Mycol.* **92**: 99. 2018.

*Basionym*: *Pseudocercospora herpotrichoides* var. *acuformis* Nirenberg, *Z. PflKrankh. PflSchutz* **88**: 244. 1981.

*Typus*: **Germany**, Göttingen, from culm base of *Secale cereale*, 1978, H. Nirenberg (**holotype** B); culture ex-holotype CBS 495.80.

*Notes*: Nirenberg (1981: 244) cited “Göttingen” as location of the holotype and CBS 495.80 as the ex-holotype culture, but under reference strains “Tübingen” was erroneously cited as locality.

***Oculimacula yallundae*** (Wallwork & Spooner) Crous & W. Gams, *Eur. J. Pl. Path.* **109**: 846. 2003. Fig. 5.

*Basionym*: *Tapesia yallundae* Wallwork & Spooner, *Trans. Brit. Mycol. Soc.* **91**: 703. 1988.

*Typus*: **Australia**, South Australia, Yallunda Flat, on *Triticum*, 18 Nov. 1986 (**holotype** K(M)233697); **isotype** DAR 58247 (ex ADW 16996). **South Africa**, Western Cape Province, Moorreesburg, on

stubble of *Triticum aestivum*, 1991, F. Bester (**epitype** designated here CBS 110665, MBT394908, preserved as metabolically inactive culture; culture ex-epitype CBS 110665).

*Notes*: *Oculimacula* was introduced to accommodate sexual morphs of the eyespot diseases of wheat and barley, previously classified in *Tapesia*, while the asexual morphs were accommodated in *Helgardia* (Crous *et al.* 2003). Following the one fungus one name system, Johnston *et al.* (2014) proposed the name *Oculimacula* for the eyespot disease complex. *Oculimacula* is herewith reduced to two species, *O. acuformis* and *O. yallundae*. The genus formed a fully or highly supported lineage for most of the loci for which sequences were available (*act*, *rpb1*, *rpb2*, *tef1*; Figs S3–S6; multigene phylogenies Figs 2, S7–S9), with the exception of ITS and LSU where it was not well resolved (Figs 1, S1, S2). The two species can be distinguished based on all individual loci analyzed (Figs S1–S6) and the multigene phylogenies (Figs 2, S7–S9). Multiplex and loop-mediated isothermal amplification (LAMP)-based molecular diagnostics have also recently been described to allow rapid species and mating-type identification of these two *Oculimacula* species (King *et al.* 2020).

***Rhyncho-brunnera*** B.A. McDonald, U. Braun & Crous, *gen. nov.* MycoBank MB838076.

*Etymology*: Composed of Rhyncho- (from the genus name *Rhynchosporium*) and Brunner (dedicated to Patrick C. Brunner, 4 July 1962 to 25 September 2019, who shared our passion for cereal fungal pathogens and was always seeking to know more about their origins and how best to define their species boundaries).

Similar to *Rhynchosporium*, but with different conidial morphology. *Conidia* solitary, subcylindrical, straight, (0–)1–3-septate, hyaline, hilum neither thickened nor darkened; conidial secession schizolytic.

*Type species*: *Rhyncho-brunnera lolii* (K.M. King *et al.*) B.A. McDonald *et al.*

*Ex-holotype culture*: CBS 135745 = IMI 502640.

***Rhyncho-brunnera lolii*** (K.M. King *et al.*) B.A. McDonald, U. Braun & Crous, *comb. nov.* MycoBank MB838077. Fig. 6.

*Basionym*: *Rhynchosporium lolii* K.M. King *et al.*, *PLoS ONE* **8**: e72536: 13. 2012.

*Typus*: **UK**, Shropshire, Newport, diseased leaves of *Lolium perenne*, May 2011, K.M. King (**holotype** IMI 502640); culture ex-holotype CBS 135745 = IMI 502640.

***Rhyncho-brunnera orthospora*** (Caldwell) B.A. McDonald, U. Braun & Crous, *comb. nov.* MycoBank MB838078. Fig. 7.

*Basionym*: *Rhynchosporium orthosporum* Caldwell, *J. Agric. Res.*, Washington **55**: 184. 1937.

*Typus*: **USA**, Wisconsin, Whitewater, on *Dactylis glomerata*, 11 May 1929, R.M. Caldwell (**holotype** BPI 415280); **isotype** WIS-f-0049657.

*Isolates examined* (reference strains): **Switzerland**, Bäretswil, on leaves of *Dactylis glomerata*, V.O. Parkinson, CBS 698.79; on leaves of *D.*



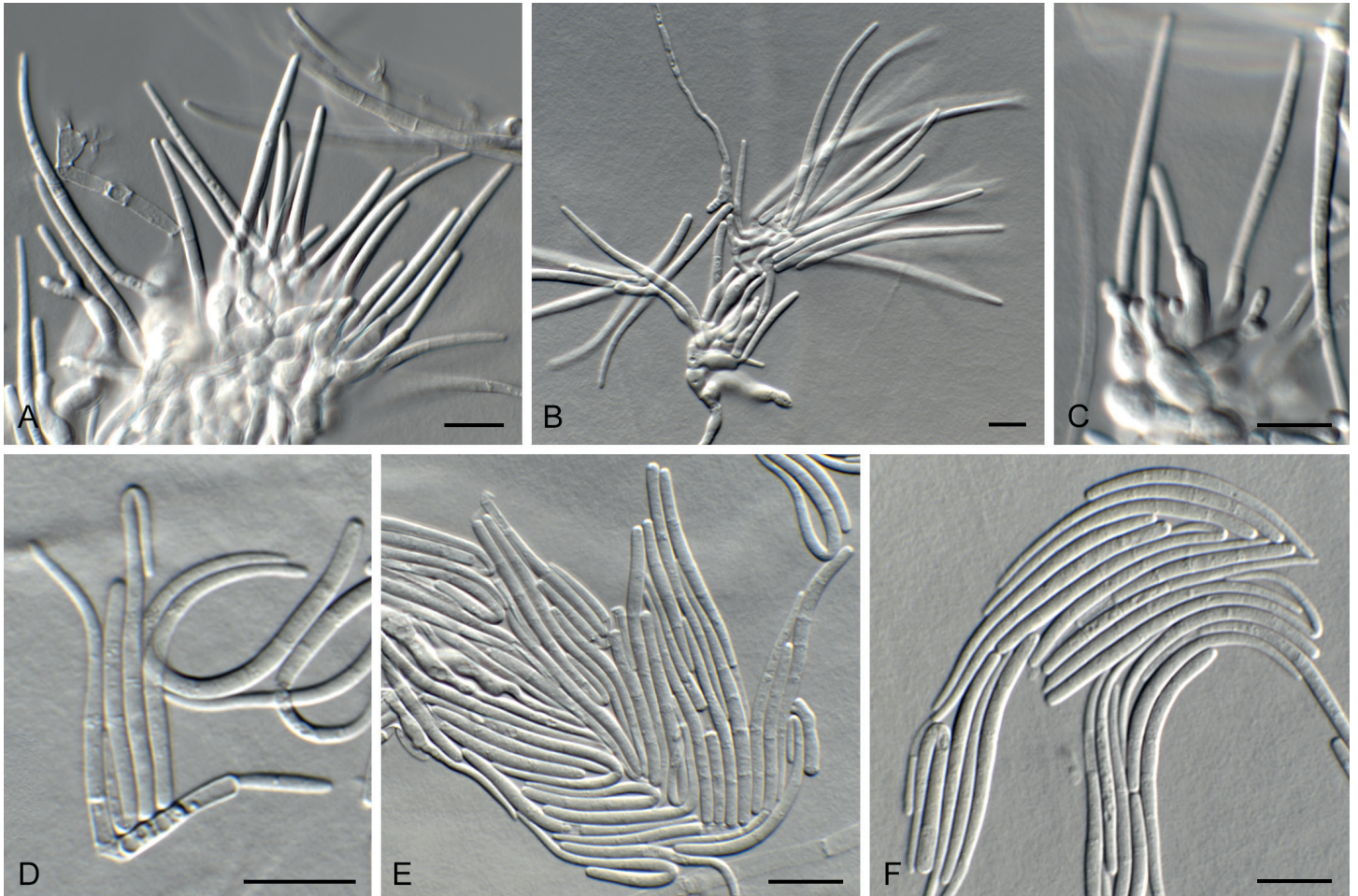


Fig. 5. *Oculimacula yallundae* (CPC 34945). A–C. Conidiogenous cells giving rise to conidia. D–F. Conidia. Scale bars = 10 µm.

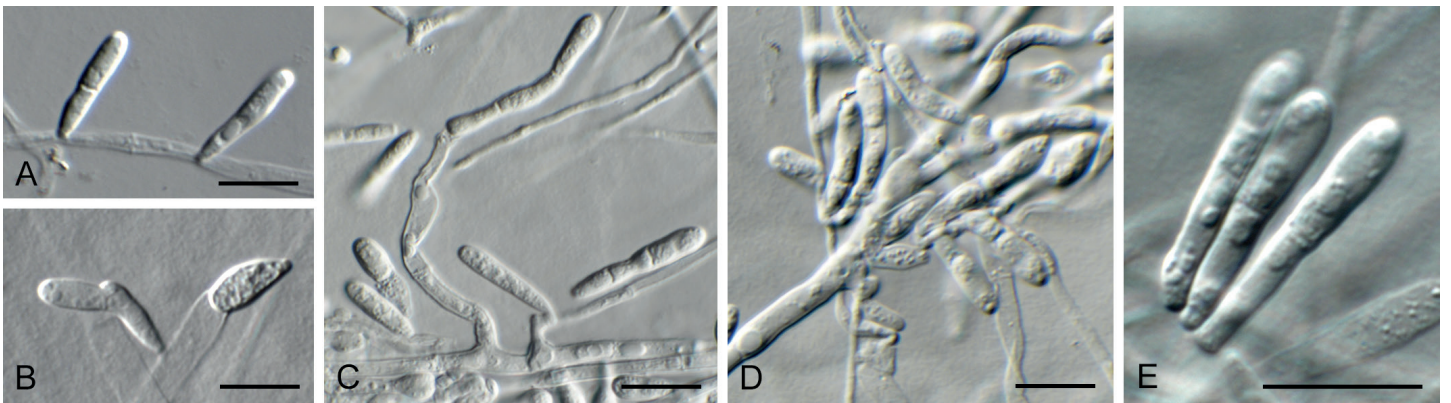


Fig. 6. *Rhynchobrunnera lolii* (CBS 135745). A–D. Hyphae with conidiogenous cells giving rise to conidia. E. Conidia. Scale bars = 10 µm.

*glomerata*, 2004, C.C. Linde, BA2.1.1 = CBS 146767. **Italy**, Aprica, on leaves of *D. glomerata*, 2004, C.C. Linde, ITA6.3 = CBS 146768.

*Description and illustration of characteristics in vivo*: Braun (1995: 256 and 257, fig. 236).

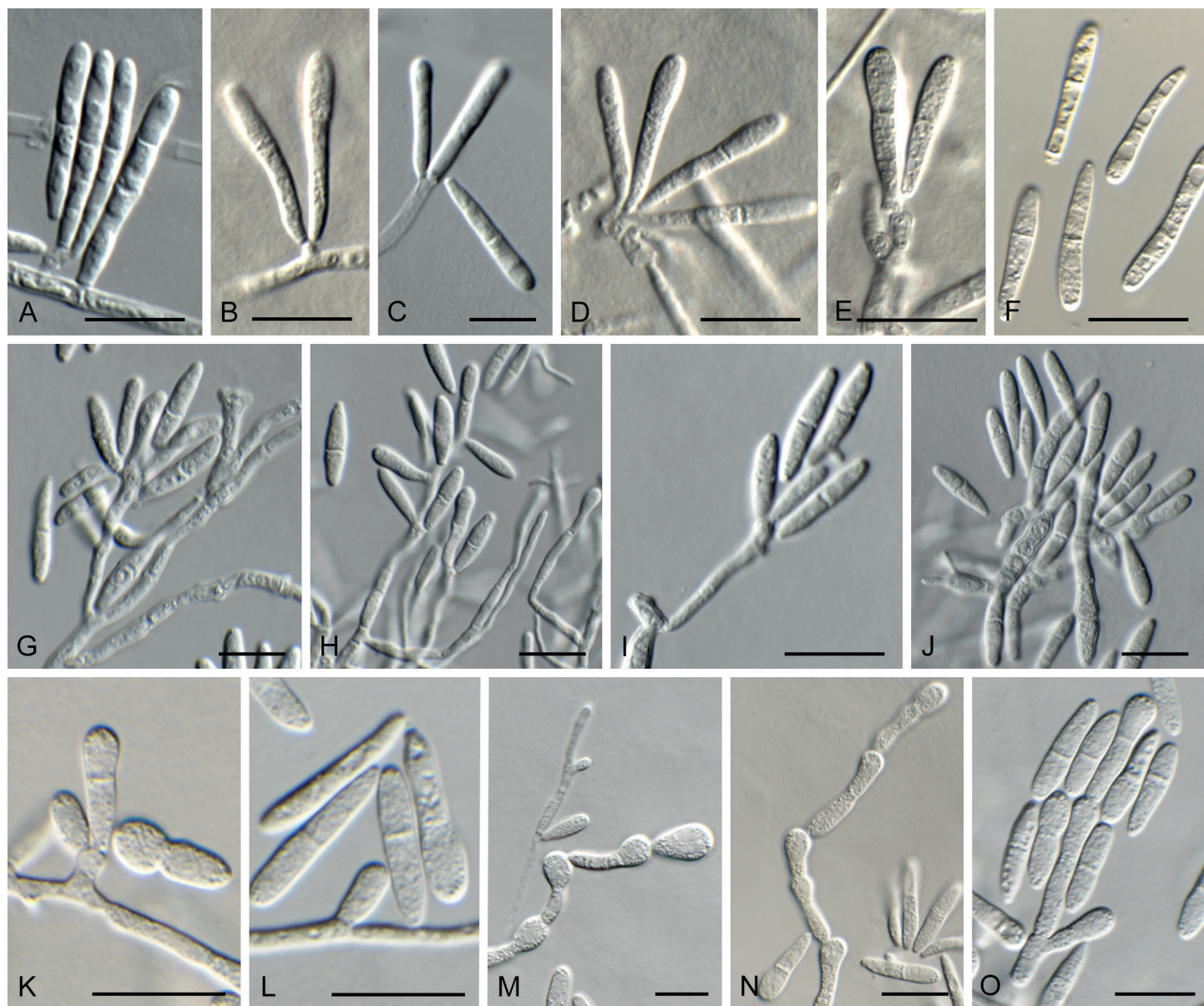
*Note*: *Rhynchobrunnera orthospora* was clearly distinguished from the genus *Rhynchosporium* using more than 380 000 genome-wide single nucleotide polymorphisms (SNPs; Mohd-Assaad *et al.* 2019). However, its distinction from *R. lolii* is controversial based on the analyses of the different gene combinations in the present study. Further studies are

required to determine if *Ra. lolii* has a wider host range, or if *Ra. orthospora* is actually a species complex. *Rhynchobrunnera lolii* was described by King *et al.* (2013) based on phylogenetic analyses of nucleotide sequences of the alpha- and beta-tubulin and ITS loci and DNA fingerprinting techniques. Their strain identifications were followed in the present study.

***Rhynchosporium*** Heinsen ex A.B. Frank, *Wochenschr. Brauerei* **14**: 518. 1897.

*Mycelium* internal, vegetative mycelium sparsely developed, sterile hyphae intraepidermal and in the mesophyll, slender, hyaline,





**Fig. 7.** *Rhynchobrunnera orthospora*. **A–F.** (CBS 698.79). **A–E.** Hyphae with conidiogenous cells giving rise to conidia. **F.** Conidia. **G–J.** (CPC 39391). **G–I.** Hyphae with conidiogenous cells giving rise to conidia. **J.** Conidia. **K–O.** (CPC 39392). **K–N.** Hyphae with conidiogenous cells giving rise to conidia. **O.** Conidia. Scale bars = 10  $\mu\text{m}$ .

septate, branched; fertile hyphae subcuticular or immediately below the outer epidermal wall, hyphae horizontally spread, colourless, septate, branched, usually 1.5–5  $\mu\text{m}$  wide, often forming ropes of parallel hyphae; single cells, groups of cells or almost all cells of long hyphae are often inflated and form small to moderately large stromatic aggregations; ropes and aggregations are often confluent in severe or old infections and form irregular, diffuse stromatic layers (“pseudo-acervuli”). Integrated, undifferentiated or swollen hyphal cells or particular cells of stromatic hyphal aggregations function as conidiogenous cells, form minute apical peg-like, subcylindrical-conical penetration tubes which perforate the cuticle and produce superficial conidia. Cuticle later often ruptured, stromatic layers erupt, exposed, superficial. *Conidiogenous cells* micronematous, mono- to polyblastic, percurrent; conidial scars inconspicuous, neither thickened nor darkened. *Conidia* solitary, subcylindrical, ellipsoid-ovoid, fusiform, curved or apex abruptly bent (with short oblique apical beak), (0–)1-septate, hyaline, hilum neither thickened nor darkened; conidial secession schizolytic (from Braun 1995).

*Type species:* *Rhynchosporium graminicola* Heinsen ex A.B. Frank

*Ex-epitype culture:* RS99CH6-C1a = ETH ZT Myc2338 = CBS 146761.

*Notes:* The names *Rhynchosporium* and *R. graminicola* have often been ascribed to Heinsen. However, these names were validated by Frank (1897). According to Frank (1897), these names were coined by his assistant E. Heinsen, but the validating description, the whole discussion, and even the complete paper were prepared and published by Frank (see Art. 46.2, 46.3; Turland *et al.* 2018). *Rhynchosporium commune* and *R. agropyri* were described by Zaffarano *et al.* (2011) based on phylogenetic analyses of nucleotide sequences of the alpha- and beta-tubulin genes and PCR-RFLP of the ITS locus. Their strain identifications were followed as references in the present study.



*Rhynchosporium agropyri* Zaffarano *et al.*, *Mycologia* **103**: 198. 2011. Fig. 8.

*Typus*: **Switzerland**, Zürich, Käferberg, from leaves of *Elymus repens* (= *Agropyron repens*), 2004, P. Zaffarano (**holotype** ZT Myc2337); culture ex-holotype RS04CH-Käferberg-4-1A4.1 = ETH ZT Myc2337 = CBS 146762.

*Additional isolates examined*: **Switzerland**, from leaves of *E. repens*, 2004, P. Zaffarano, K4\_5A1 = CBS 146769; from leaves of *E. repens*, 2005, P. Zaffarano, Daen1.1.2 = CBS 146770.

*Notes*: *Rhynchosporium agropyri* was introduced for a species occurring on *Agropyron* spp., and the apparent paraphyly observed for species of *Rhynchobrunnera* and *Rhynchosporium* in for example Figs 2, S1–S9 is most likely due to the fact that the strains were identified using alpha- and beta-tubulin sequences in the original publications (Zaffarano *et al.* 2011, King *et al.* 2013), two gene regions not included in the present study.

*Rhynchosporium graminicola* Heinsen ex A.B. Frank, *Wochenschr. Brauerei* **14**: 518. 1897. Fig. 9.

*Synonymy*: *Ramularia hordei* McAlpine, *Proc. Linn. Soc. New South Wales* **27**: 379. 1902.

*Rhynchosporium commune* Zaffarano, B.A. McDonald & C.C. Linde, *Mycologia* **103**: 196. 2011.

*Typus*: **Germany**, on barley, Frank (1897: 519, unnumbered drawing), **lectotype**, designated by Braun (2016: 40). **Switzerland**, Cugy, Canton Vaud, from leaves of *Hordeum vulgare*, 1999 (**epitype** designated by Braun (2016: 40), ZT Myc2338); culture ex-epitype, RS99CH6-C1a = ETH ZT Myc2338 = CBS 146761.

*Notes*: For typification details and discussion of synonymy, see Braun (2016). For additional isolates examined, see Table 1.

*Rhynchosporium secalis* (Oudem.) Davis, *Trans. Wis. Acad. Sci. Arts Lett.* **19**(2): 713. 1919. Fig. 10.

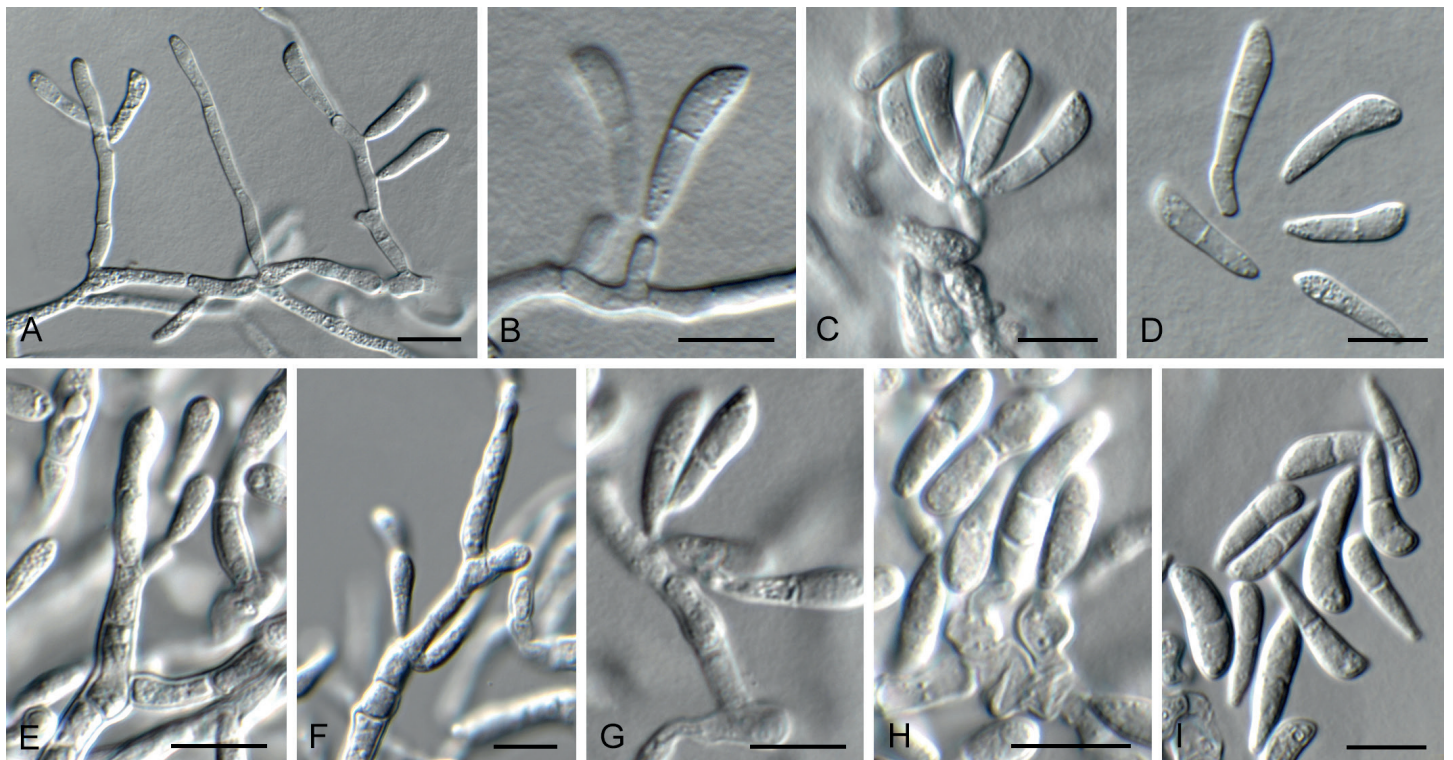
*Basionym*: *Marssonina secalis* Oudem., *Med. Kon. Akad. v. Wetensch.* **3**: 88. 1897.

*Typus*: **Netherlands**, on leaves of *Secale cereale*, *R. Bos* (**holotype** missing, not found in L). **Switzerland**, Reckenholz-Oerlikon, on leaves of *Secale cereale*, 15 Jun. 1952, *E. Müller* (**neotype** CBS 385.52 designated here, MBT394909, preserved as metabolically inactive culture; culture ex-neotype CBS 385.52).

*Additional isolates examined*: **Russia**, on leaves of *Secale cereale*, 2003, P. Zaffarano, RUB2.3 = CBS 146772. **Switzerland**, ×*Triticosecale*, 2004, P. Zaffarano, CH4\_4b1 = CBS 146771.

*Description and illustration of characteristics in vivo*: Braun (1995: 255 and 257, fig. 235).

*Notes*: *Rhynchosporium* includes several species that cause leaf scald diseases on cereal and grass hosts, and express a high level of host specificity, namely *R. graminicola* (colonising *Hordeum glaucum*, *H. leporinum*, *H. murinum*, *H. spontaneum*, *H. vulgare* and *Bromus diandrus*), *R. agropyri* (*Elymus caninus* and *E. repens*) and *R. secalis* (*Secale cereale* and ×*Triticosecale*) (King *et al.* 2013). For related species previously treated in *Rhynchosporium*, see the treatment of *Rhynchobrunnera* above. *Rhynchosporium agropyri*, *R. graminicola* and *R. secalis* are phylogenetically very closely related based on the genes used here (Figs 1, 2, S1–S9). The species can be distinguished to some degree based on ITS (Fig. S1). Previous studies have used



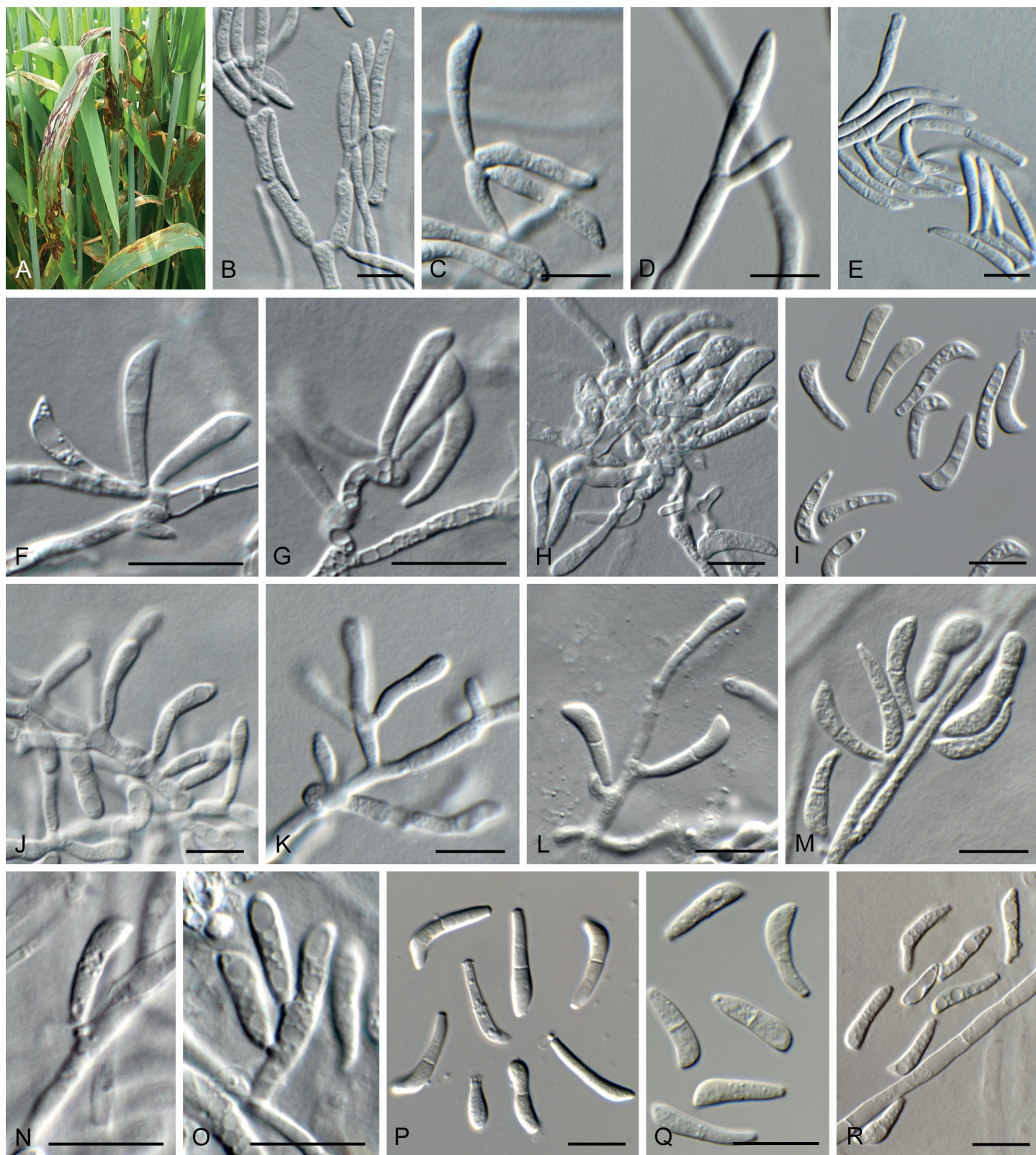
**Fig. 8.** *Rhynchosporium agropyri*. **A–D.** (CPC 39393). **A–C.** Hyphae with conidiogenous cells giving rise to conidia. **D.** Conidia. **E–I.** (CPC 39394). **E–H.** Hyphae with conidiogenous cells giving rise to conidia. **I.** Conidia. Scale bars = 10 µm.



RAPDs and species-specific PCR diagnostic tests (e.g. King *et al.* 2013) or a combination of alpha-tubulin, beta-tubulin and ITS sequences for species delimitation (Zaffarano *et al.* 2008, 2011). More recent studies used approximately 380 000 genome-wide SNPs to confirm species boundaries (Mohd-Assaad *et al.* 2019).

*Septogloeum* Sacc., *Michelia* 2: 11. 1880.

*Mycelium* immersed, branched, septate, hyaline. *Conidiomata* acervular, epidermal to subepidermal, separate or confluent, formed of pale brown thin-walled pseudoparenchyma. Dehiscence irregular. *Conidiophores* short, stout, 1–2-septate,



**Fig. 9.** *Rhynchosporium graminicola*. **A.** Disease symptoms on *Hordeum vulgare*. **B–E.** (CPC 39388). **B–D.** Hyphae with clusters of conidiogenous cells giving rise to conidia. **E.** Conidia. **F–I.** (CBS 135932). **F–H.** Hyphae with conidiogenous cells giving rise to conidia. **I.** Conidia. **J–M.** (CBS 483.50). **J–L.** Hyphae with conidiogenous cells giving rise to conidia. **M.** Conidia. **N–R.** (CBS 385.52). **N–Q.** Hyphae with conidiogenous cells giving rise to conidia. **R.** Conidia. Scale bars = 10 µm.





Fig. 10. *Rhynchosporium secalis* (CPC 39385). A, B. Hyphae with conidiogenous cells giving rise to conidia. C. Conidia. Scale bars = 10 µm.

hyaline, smooth, branched at the base, formed from the upper pseudoparenchyma. *Conidiogenous cells* enteroblastic, phialidic, discrete or integrated, determinate, cylindrical, doliiform to obpyriform, hyaline, smooth, channel wide, collarette minimal, periclinal wall thickened. *Conidia* hyaline, 1–3-euseptate, thin-walled, smooth, eguttulate, base truncate, apex obtuse, straight or curved, constricted, obovoid (from Sutton 1980).

*Type species*: *S. carthusianum* (Sacc.) Sacc.

*Ex-type culture*: No culture available.

*Notes*: Although some of the isolates from cereals studied here were formerly identified as species of *Septogloeum*, Sutton & Pollack (1974) restricted the genus *Septogloeum* to two species, *S. carthusianum* and *S. thomsonianum*. DNA data of the type species (on *Euonymus europaeus*, Europe) need to be obtained to facilitate a revision of *Septogloeum*.

***Spermospora*** R. Sprague, *Mycologia* **40**: 177. 1948.

*Mycelium* internal, hyphae hyaline, septate, branched, slender, forming solitary to aggregated (sometimes stromatic) swollen vesicular intraepidermal, sometimes substomatal cells, shape and size variable, hyaline. Most of these vesicles functioning as *conidiogenous cells* ("mother cells"), conical to ampulliform, apically attenuated, forming minute, narrow penetration tubes which perforate the cuticle of the host plant or emerge through the stomatal opening; two or even more penetration tubes may occasionally be formed from a single vesicle or minute tubes arise from narrow, hardly differentiated hyphal cells;

penetration tubes or attenuated apical parts of conidiogenous cells bearing a single terminal, holoblastic conidium; penetration tubes sometimes becoming inflated above the host surface and forming a single or rarely two conidia; conidial scars inconspicuous, neither thickened nor darkened. *Macroconidia* solitary, scolecosporous, acicular-fusiform, obclavate, straight to curved, hyaline, euseptate, smooth, usually tapering towards the apex, basal cells sometimes with a short lateral or sub-basal narrow appendage, hilum more or less truncate, unthickened, hyaline; conidial secession schizolytic (from Braun 1995). *Microconidia* subcylindrical, hyaline, smooth, 0(–1)-septate, base truncate, apex obtuse, straight.

*Type species*: *Spermospora subulata* (R. Sprague) R. Sprague

*Typus*: **USA**, Oregon, Main Divide Trail, Ochoco Nat. Forest, on *Melica subulata*, 21 Aug. 1916, Ingram 606 (**holotype** OSC 10.669); **isotypes** BPI 420956, FH 01012456, NY 01042813. No culture available.

*Notes*: As treated here, the genus *Spermospora* is paraphyletic, awaiting the recollection of the type species, *Sp. subulata*. Although we suspect that *Sp. subulata* would be allied to *Sp. ciliata* and *Sp. zae* (*Spermospora s.str.*), this remains to be elucidated.

***Spermospora arrhenatheri*** Crous, *sp. nov.* MycoBank MB838079. Fig. 11.

*Etymology*: Name refers to the genus *Arrhenatherum*, to which the host of this species belongs.

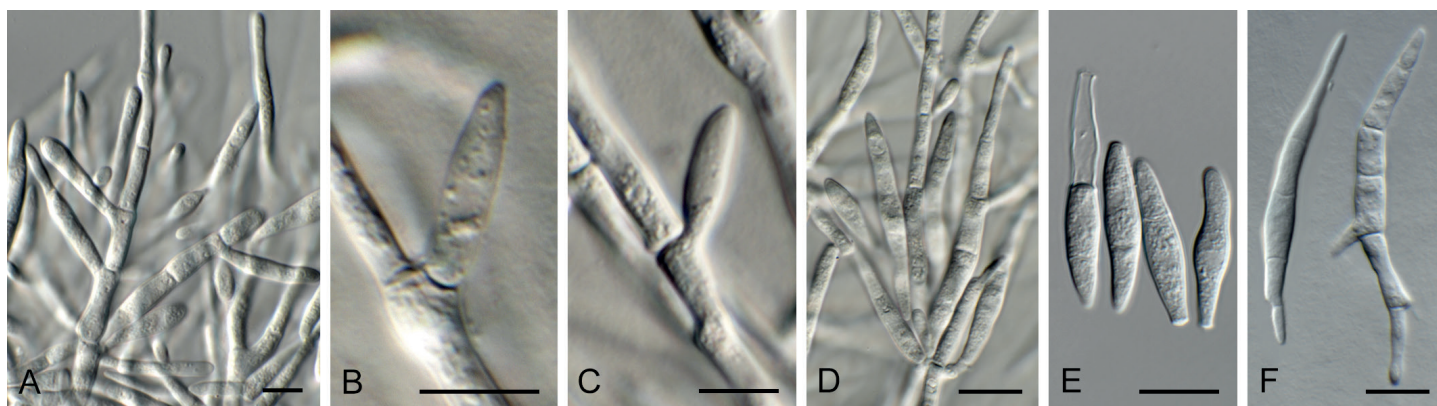


Fig. 11. *Spermospora arrhenatheri* (CBS 320.68). A–D. Hyphae with conidiogenous cells giving rise to conidia. E, F. Conidia. Scale bars = 10 µm.



*Conidiophores* mostly reduced, 2 µm diam, conidiogenous loci formed directly on hyphae. *Conidia* hyaline, smooth, granular, (2–)3(–4)-septate, fusoid to fusoid-obclavate, (30–)40–50(–60) × (4–)5–6 µm; basal appendage arising above the hilum, lateral, pointing downwards, at times appearing as a germ tube with a septum separating it from the conidium body, 5–15 × 2 µm, developing while still attached to the conidiogenous cell.

**Typus:** Germany, Kiel-Kitzeberg, on *Arrhenatherum elatius*, Jul. 1966, U.G. Schlösser, No. 16 (**holotype** CBS 320.68, preserved as metabolically inactive culture; culture ex-holotype CBS 320.68).

**Notes:** The culture of *Sp. arrhenatheri* was originally deposited as *Septogloeum oxysporum* (now *Cheilaria agrostidis*), a fungus causing blotch and tar spot of various grasses (conidiomata acervular, conidia hyaline, 1–3-septate, obovoid; Mäkelä & Koponen 1976, Sutton 1980), which is quite different from the fungus treated here. The species formed a single-strain lineage for most of the loci for which a sequence was available (ITS, *act*, *rpb2*; Figs S1, S3, S5; multigene phylogenies Figs 2, S7–S9), with the exception of LSU where it was not well resolved (Figs 1, S2).

***Spermospora ciliata*** (R. Sprague) Deighton, *Trans. Br. mycol. Soc.* **51**: 44. 1968. Figs 12, 13.

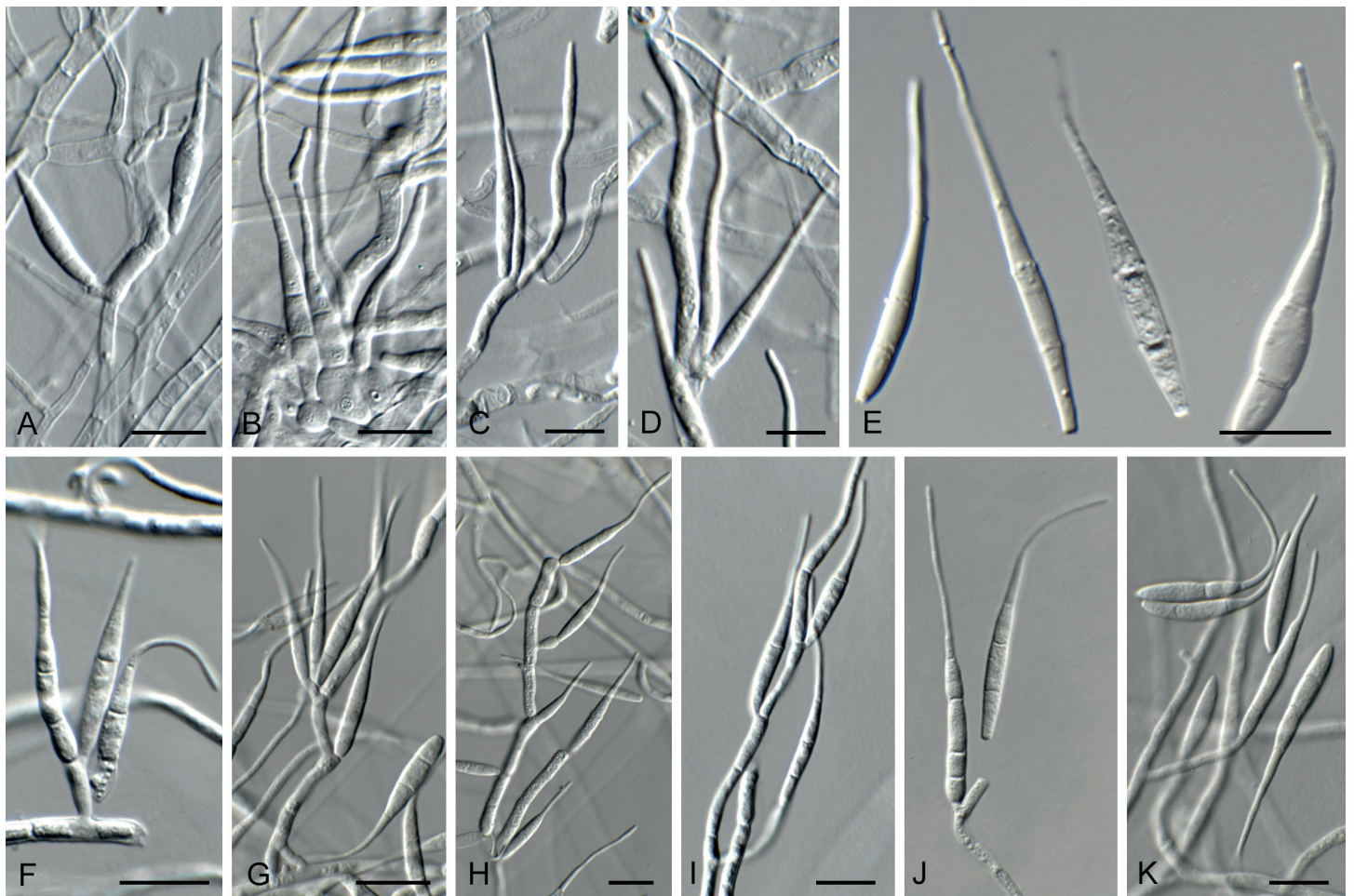
**Basionym:** *Spermospora subulata* f. *ciliata* R. Sprague, *Mycologia* **41**: 495. 1949.

*Mycelium* of hyaline, smooth, branched, septate, 2–4 µm diam hyphae. *Conidiophores* reduced to hyphae forming conidiogenous loci, or solitary, erect, hyaline, smooth, subcylindrical, 0–2-septate, 10–20 × 2.5–3.5 µm. *Conidiogenous cells* terminal, integrated, subcylindrical, 5–10 × 2.5–3 µm; proliferating sympodially. *Conidia* solitary, hyaline, smooth, guttulate, fusoid to fusoid-obclavate, straight to curved, apical cell forming a flexuous appendage, 1–2(–3)-septate, (20–)30–40(–47) × (2.5–)3 µm; apical cell (incl. flexuous appendage) 11–25 µm long, base truncate, 1.5–2 µm diam, not thickened nor darkened (CBS 135.38).

*Conidia* solitary, hyaline, smooth, guttulate, fusoid, rarely fusoid-obclavate, straight to curved, apical cell forming a flexuous appendage, 1–2(–3)-septate, (20–)37–50(–65) × 3–3.5(–4) µm; apical cell (incl. flexuous appendage) 17–45 µm long, base truncate, 1.5–2 µm diam, not thickened nor darkened; basal appendage arising laterally, above the basal hilum, at times separated by a septum (CBS 287.69).

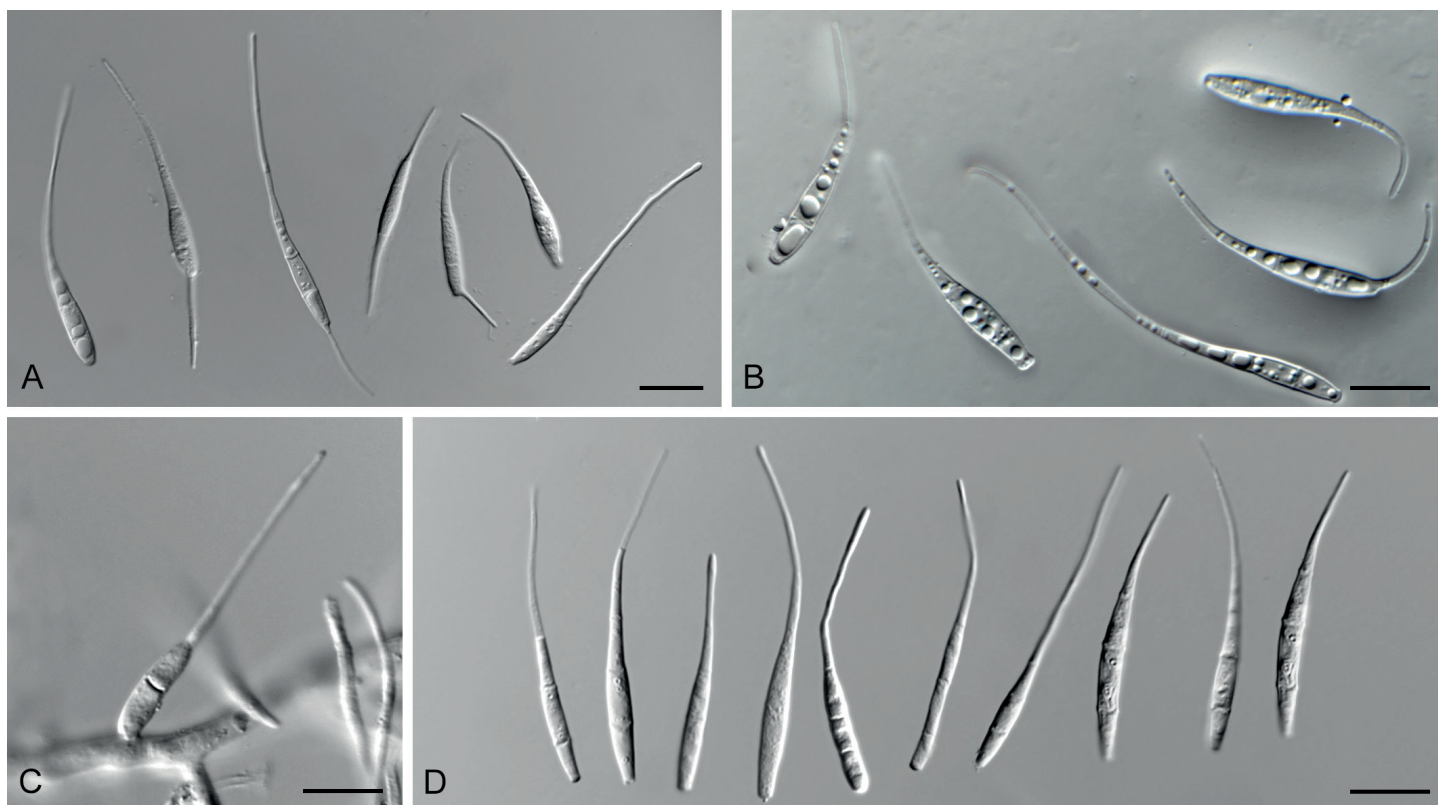
*Conidiophores* mostly reduced to loci occurring directly on hyphae, 2 µm diam. *Conidia* hyaline, smooth, fusoid to obclavate-fusoid, 3(–4)-septate, (33–)35–60(–80) × 3(–3.5) µm, apical cell (incl. flexuous appendage) (20–)30–55 µm long (CBS 316.68).

**Typus:** USA, Wyoming, Teton Pass, on *Agrostis stolonifera*, 13 Aug. 1948, Sprague et al. (**holotype** WSP 20123).



**Fig. 12.** *Spermospora ciliata*. **A–E.** (CBS 135.38). **A–D.** Hyphae with conidiogenous cells giving rise to conidia. **E.** Conidia. **F–K.** (CBS 316.68). **F–J.** Hyphae with conidiogenous cells giving rise to conidia. **K.** Conidia. Scale bars = 10 µm.





**Fig. 13.** *Spermospora ciliata* (CBS 285.69). **A, B.** Conidia (CBS 287.69). **C.** Conidium developing on conidiogenous locus. **D.** Conidia (CBS 285.69). Scale bars = 10  $\mu\text{m}$ .

*Isolates examined:* **Germany**, Kiel-Kitzeberg, on *Festuca arundinacea*, U.G. Schlösser, No. 54, May 1967, CBS 285.69; Kr. Plön, Mönkeberg, on *Festuca heterophylla*, U.G. Schlösser, No. 85, Aug. 1967, CBS 287.69; Kiel-Kitzeberg, on *Festuca rubra*, May 1967, U.G. Schlösser, No. 59, culture CBS 316.68. **USA**, Oregon, Halsey, on *Festuca rubra*, 1937, R. Sprague, OSC 10669, CBS 135.38.

*Description and illustration of characteristics in vivo:* Braun (1995: 242, fig. 224 and 243).

*Notes:* The genus *Spermospora* is similar to *Rhynchosporium* in that it also has immersed, swollen conidiogenous cells with minute tubes that penetrate the cuticle and bear solitary non-scolecosporous conidia (Braun 1995). The type species, *S. subulata*, has narrow conidia, with those in the holotype being obclavate, 1–2(–4)-septate, (15–)20–30(–65)  $\times$  3–4.5  $\mu\text{m}$  (Braun 1995).

Isolate CBS 135.38 was deposited by R. Sprague in 1937 as *S. subulata* (on *Festuca rubra*, in Halsey, Oregon). However, a few years later, Sprague described *S. subulata* f. *ciliata*, which was later elevated to species level as *S. ciliata*. Conidia of *S. ciliata* (on *Agrostis alba*, Wyoming, USA) are reported to be fusoid to obclavate-fusoid, 20–75  $\times$  (2–)3–6(–8)  $\mu\text{m}$ , 2–4-septate; apical cell with appendage 5–35  $\mu\text{m}$  long, with lateral filiform appendage 5  $\mu\text{m}$  long (Braun 1995). Isolate CBS 135.38 is thus more appropriately placed in *S. ciliata* than *S. subulata*. Braun (1995) was of the opinion that *S. subulata* should be confined to species occurring on *Melica* in the USA, having narrowly obclavate, 1–2-septate conidia, and that isolates from other hosts probably belonged to *S. ciliata* (conidia fusoid to obclavate-fusoid, 2–4-septate, the basal cell occasionally having a narrow, lateral, filiform appendage). Isolates of *S. ciliata* formed a fully or highly supported sister lineage to *S. zeae* in analyses of most

of the loci for which sequences were available (ITS, *act*, *rpb1*, *rpb2*, *tef1*; Figs S1, S3–S6; multigene phylogenies Figs 2, S7–S9).

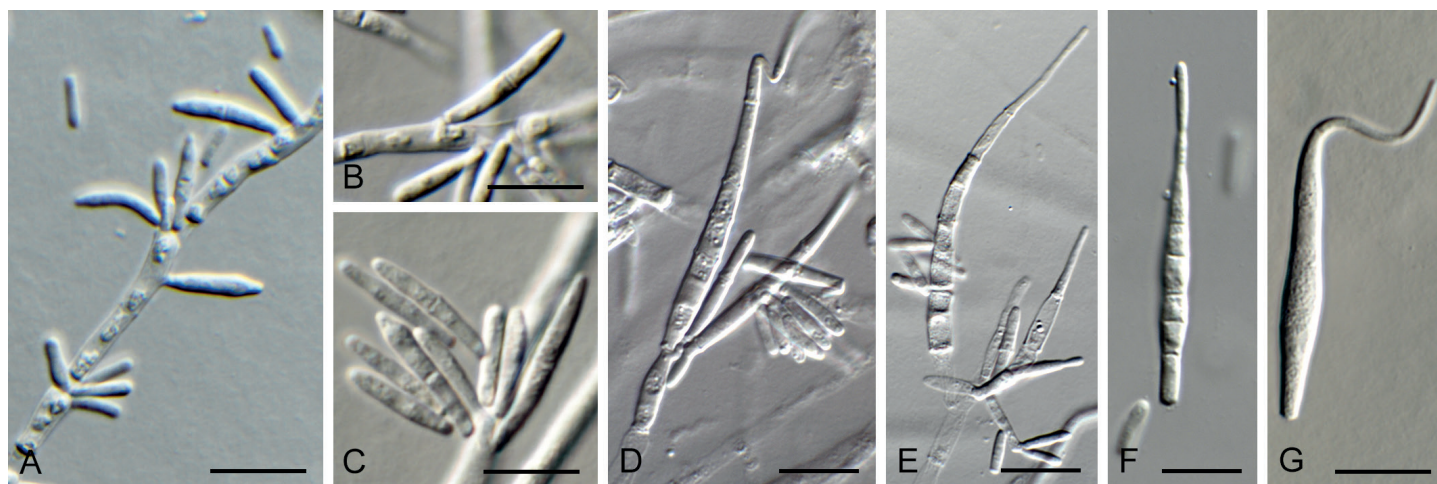
***Spermospora loliiphila* Crous, sp. nov.** MycoBank MB838080. Fig. 14.

*Etymology:* Name composed of *Lolium*, to which the host of this species belongs, and *-philus* (-loving).

*Mycelium* consisting of hyaline, smooth, branched, septate, 2–4  $\mu\text{m}$  diam hyphae. Species dimorphic. Microconidial morph: *Microconidiophores* reduced to microconidiogenous cells or loci formed directly on hyphae, or erect, subcylindrical, 5–15  $\times$  2–3  $\mu\text{m}$ , proliferating sympodially, giving rise to mucoid conidial masses. *Microconidia* subcylindrical, hyaline, smooth, 0(–1)-septate, base truncate, apex obtuse, straight, (8–)10–13(–17)  $\times$  2  $\mu\text{m}$ . *Macroconidiophores* subcylindrical, hyaline, smooth, 0–2-septate, unbranched, 10–20  $\times$  2–3  $\mu\text{m}$ . *Macroconidiogenous cells* integrated, hyaline, smooth, 5–10  $\times$  2–3  $\mu\text{m}$ , proliferating sympodially. *Macroconidia* hyaline, smooth, guttulate, fusoid, straight to slightly curved, 3(–5)-septate, (25–)35–55(–65)  $\times$  3(–4)  $\mu\text{m}$ ; apical cell (incl. flexuous apical appendage) 10–20  $\mu\text{m}$  long.

*Typus:* **New Zealand**, Palmerston North, on *Lolium perenne*, Aug. 1964, U.G. Schlösser, No. 124 (**holotype** CBS 286.69, preserved as metabolically inactive culture; culture ex-holotype CBS 286.69).

*Notes:* Isolate CBS 286.69 (from *Lolium perenne*, New Zealand), was deposited as *S. subulata* [conidia obclavate, 1–2(–4)-septate, (15–)20–30(–65)  $\times$  3–4.5  $\mu\text{m}$ ; Braun 1995]. It differs from *S. subulata* in having fusoid macroconidia, and a microconidial morph with aseptate conidia, and from *S. ciliata* [conidia fusoid



**Fig. 14.** *Spermospora loliiphila* (CBS 286.69). **A.** Hyphae with conidiogenous loci giving rise to microconidia. **B, C.** Microconidia. **D, E.** Macro- and microconidia. **F, G.** Macroconidia. Scale bars = 10  $\mu$ m.

to obclavate-fusoid, 2–4-septate, 20–75  $\times$  (2–)3–6(–8)  $\mu$ m; Braun 1995] in having narrower macroconidia and a microconidial morph. Furthermore, it differs from *S. lolii* (from *Lolium perenne*, Ireland; conidia fusoid to obclavate-fusoid, 2–7-septate, 35–70  $\times$  3.5–4.5  $\mu$ m; Braun 1995) based on its smaller macroconidia with less septa. The species formed a single-strain lineage for most of the loci for which a sequence was available (ITS, *act*, *rpb2*, *tef1*; Figs S1, S3, S5, S6; multigene phylogenies Figs 2, S7–S9), with the exception of LSU where it was not well resolved (Figs 1, S2). In the ITS phylogeny (Fig. S1), it is basal to *Spermospora zaeae* and *S. ciliata* with a low posterior probability value. It does not form a monophyletic group with *Spermospora zaeae* and *S. ciliata* based on *act* (Fig. S3), *rpb2* (Fig. S5), *tef1* (Fig. S6) and could represent a cryptic genus in this complex.

***Spermospora zaeae*** Crous, *sp. nov.* MycoBank MB838081. Fig. 15.

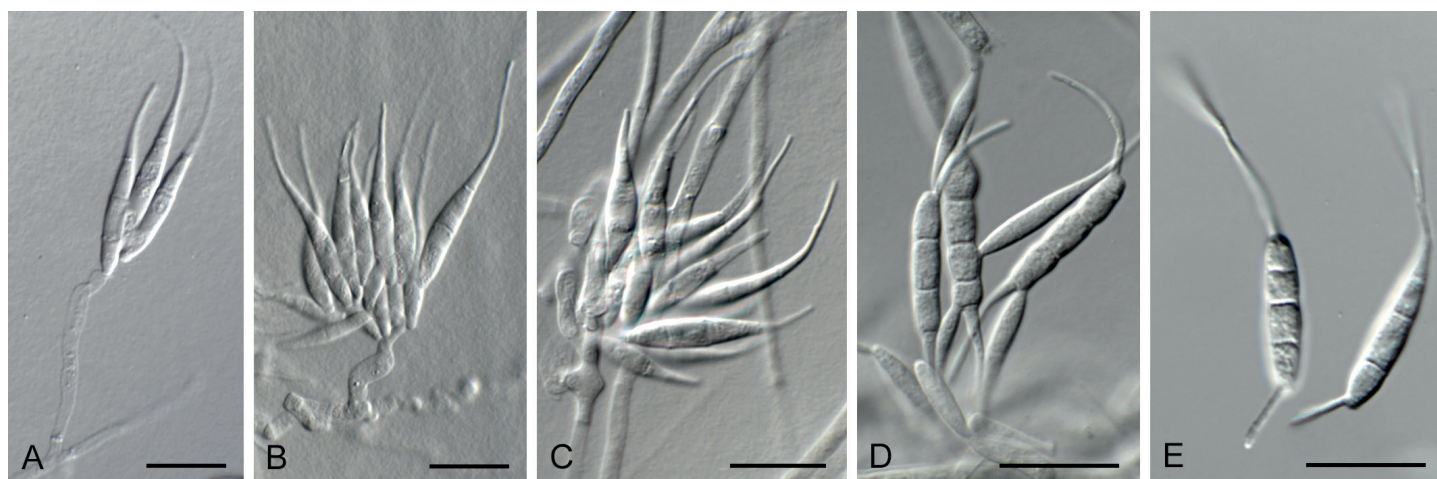
**Etymology:** Name refers to the genus *Zea*, from which this species was isolated.

**Mycelium** consisting of hyaline, smooth, septate, branched, 2.5–3  $\mu$ m diam hyphae. **Conidiophores** reduced to conidiogenous

cells or solitary loci, erect, subcylindrical, hyaline, smooth, 0–1-septate, unbranched, 10–25  $\times$  2–3  $\mu$ m. **Conidiogenous cells** terminal, integrated, subcylindrical, smooth, hyaline, 8–10  $\times$  2–3  $\mu$ m, proliferating sympodially. **Conidia** aggregating in mucoid clusters, fusoid to obclavate-fusoid, hyaline, smooth, guttulate, (0–)3-septate with truncate hilum, 2  $\mu$ m diam, and apex tapering to a long flexuous apical appendage terminating in subobtuse end, (25–)30–40(–45)  $\times$  (2.5–)3(–4)  $\mu$ m; apical cell (incl. appendage) (7–)15–22  $\mu$ m long; basal appendage aseptate, cellular, lateral, pointing downwards, arising just above basal hilum, at times appearing as a germ tube from the basal hilum. Older conidia undergoing microcyclic conidiation, with conidia developing several lateral appendages, also arising from central cells of the conidium body, and the apical appendage can even branch dichotomously.

**Typus:** Switzerland, Zürich, endophyte in *Zea mays*, E. Müller ETH 8867 (**holotype** CBS 306.79, preserved as metabolically inactive culture; culture ex-holotype CBS 306.79).

**Note:** *Spermospora zaeae* formed a single-strain lineage sister to *Spermospora ciliata* for most of the loci for which a sequence was available (ITS, *act*, *rpb2*; Figs S1, S3, S5; multigene phylogenies



**Fig. 15.** *Spermospora zaeae* (CBS 306.79). **A–D.** Hyphae with conidiogenous cells giving rise to conidia. **E.** Conidia. Scale bars = 10  $\mu$ m.



Figs 2, S7–S9), with the exception of LSU where it was not well resolved (Figs 1, S2).

**Vanderaaea** Crous, *gen. nov.* MycoBank MB838082.

**Etymology:** Named in honour of the Dutch mycologist Hubertus Antonius “Huib” van der Aa (5 July 1935 – 7 May 2017), who was a mycologist dealing with coelomycetous fungi at the “Centraalbureau voor Schimmelcultures”, and also collected and isolated this fungus.

**Conidiomata** sporodochial, round, erumpent, green-brown, giving rise to a mucoid conidial mass. **Conidiophores** reduced to conidiogenous cells formed on a stroma of pale brown pseudoparenchymatal cells, smooth, ampulliform to subglobose, proliferating holoblastically. **Conidia** solitary, hyaline, smooth, 0–1-septate, fusoid, flexuously curved, apical cell developing into a long flexuous apical appendage with subobtuse tip, basal cell tapering towards a truncate hilum.

**Type species:** *Vanderaaea ammophilae* Crous

**Vanderaaea ammophilae** Crous, *sp. nov.* MycoBank MB838083. Fig. 16.

**Etymology:** Name reflects *Ammophila*, the host genus it was collected from.

**Conidiomata** up to 350 µm diam, sporodochial, round, erumpent, green-brown, giving rise to a mucoid conidial mass. **Conidiophores** reduced to conidiogenous cells, pale brown, smooth, ampulliform to subglobose, 4–6 × 2–3 µm, proliferating holoblastically. **Conidia** solitary, hyaline, smooth, 0–1-septate, septum submedian, fusoid, flexuously curved, apical cell developing into a long flexuous apical appendage with subobtuse tip, basal cell tapering towards truncate hilum, 1 µm diam; conidia (20–)21–22(–24) × (1.5–)2 µm, apical cell 11–14 µm long, basal cell 7–10 µm long.

**Typus:** **Netherlands**, Texel, “De Krim”, on dead leaves of *Ammophila arenaria*, 26 Oct 1968, H.A. van der Aa (**holotype** CBS H-18325; culture ex-holotype CBS 886.68).

**Notes:** Isolate CBS 886.68 was originally identified as *Spermospora avenae*, but is quite distinct in having sporodochial

conidiomata, and 0–1-septate, flexuously curved conidia. The species is distinct from all species treated here as belonging to *Acarosporales* (*Lecanoromycetes*) by forming sporodochia with curved, 0–1-septate conidia (Fig. 1, part 1).

***Ypsilina*** J. Webster *et al.*, *Canad. J. Bot.* **76**: 1658. 1999.

**Conidiophores** terminal, simple or branched, hyaline, septate. **Conidiogenous cells** terminal, proliferating sympodially or percurrently at the apex. **Conidia** Y-shaped, terminal, single, variously branched, with arms long-conoid, septate, with acute apices, bases truncate, or with a subulate basal extension; branches sequential, opposite, alternate, dorsal. Synasexual morph phialidic, forming hyaline, aseptate conidia.

**Type species:** *Ypsilina graminea* (Ingold *et al.*) Descals *et al.*

**Ex-epitype culture:** CBS 114630.

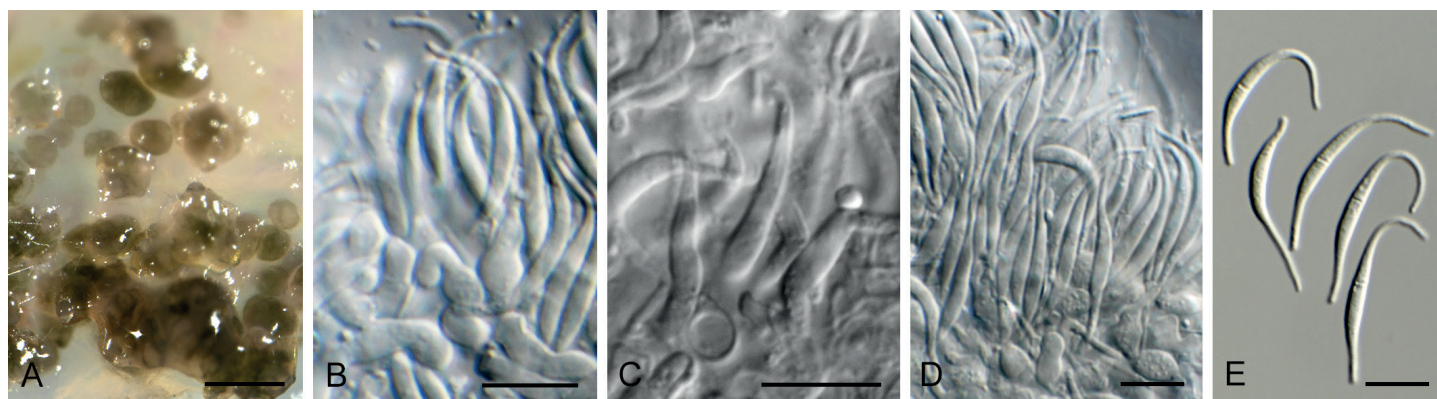
***Ypsilina graminea*** (Ingold *et al.*) Descals *et al.*, *Canad. J. Bot.* **76**: 1659. 1999 (1998). Fig. 17.

**Basionym:** *Volucrispora graminea* Ingold *et al.*, *Trans. Brit. Mycol. Soc.* **51**: 325. 1968.

**Typus:** **UK**, England, county of Cumbria (former Cumberland), Aira Force, undated, isolated from freshwater foam (**holotype** IMI 123908); **UK**, on roots of *Triticum aestivum*, 10 Nov. 2001, H. Kwasna (**epitype** designated here CBS 114630, MBT394914, preserved as metabolically inactive culture; culture ex-epitype CBS 114630).

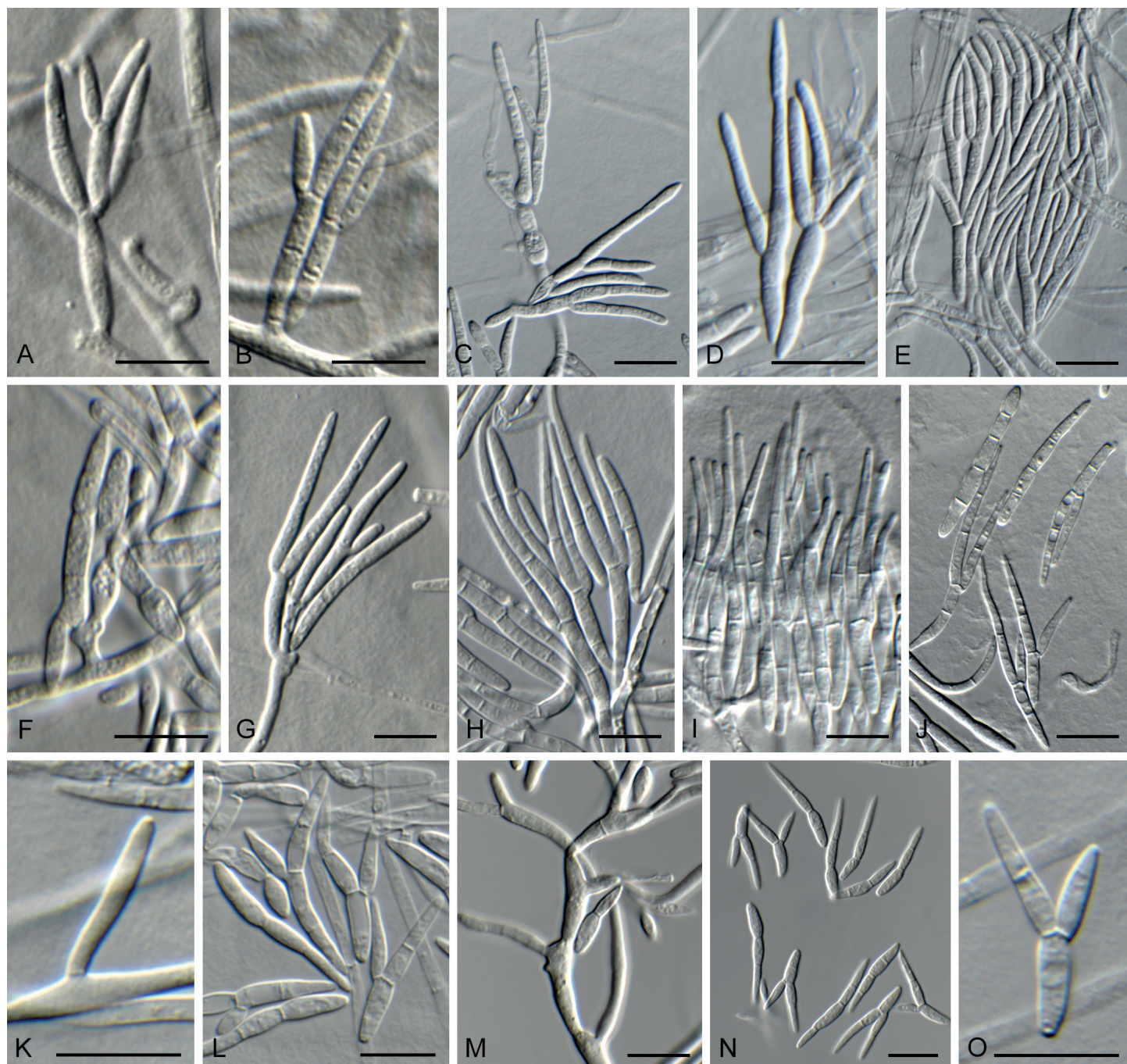
**Additional cultures examined:** **Antarctica**, King George, Jubany, on a leaf of *Deschampsia antarctica*, 1991, C. Möller, No. 17/10, CBS 691.92; King George, Arctowski, on a lichen, 1991, C. Möller, No. 42/10, CBS 692.92. **Germany**, Kr. Husum, Hollingstedt, on *Holcus lanatus*, U.G. Schlösser, No. 231, CBS 895.72.

**Notes:** The species has been isolated from freshwater foam in the UK, but also from grass leaves and roots of *Triticum aestivum* and *Holcus lanatus*, and as shown here, from a lichen in Antarctica. However, its ecology remains largely unknown (Descals *et al.* 1998). *Ypsilina graminea* formed a fully or highly supported lineage in the analyses of most of the loci for which sequences were available (ITS, *act*, *rpb1*, *rpb2*, *tef1*; Figs S1, S3–S6; multigene phylogenies Figs 2, S7–S9), with the exception of



**Fig. 16.** *Vanderaaea ammophilae* (CBS 886.68). **A.** Sporulating colony on oatmeal agar. **B–D.** Conidiogenous cells giving rise to conidia. **E.** Conidia. Scale bars = 10 µm.





**Fig. 17.** *Ypsilina graminea*. **A–E.** (CBS 691.92) **A–C.** Hyphae with conidiogenous cells giving rise to conidia. **D, E.** Conidia. **F–J.** (CBS 692.92) **F–H.** Hyphae with conidiogenous cells giving rise to conidia. **I, J.** Conidia. **K–O.** (CBS 114630). **K–M.** Hyphae with conidiogenous cells giving rise to conidia. **N, O.** Conidia. Scale bars = 10  $\mu$ m.

LSU where it was not well resolved (Figs 1, S2). Some intraspecific variation exists for this species: in ITS up to five substitutions and one indel, in *act* up to eight substitutions and one indel; in *rpb1* up to 17 substitutions; in *rpb2* up to 49 substitutions. The similarity of the *tef1* sequences of the ex-type strain ranges from 90 % (CBS 895.72) to 83 % (CBS 692.92), whereas the LSU sequences of the four analysed strains were identical.

## DISCUSSION

The present study aimed to resolve the status of genera for the well-known cereal pathogens *Oculimacula*, *Rhynchosporium* and *Spermospora*. In the process, we had to consider the

genera *Septogloeum* and *Ypsilina*, which were found to be phylogenetically related.

The phylogenetic and morphological differences among species of *Rhynchosporium* (leaf blotch of cereals) have been well documented in papers dealing with these taxa (Zaffarano *et al.* 2011, King *et al.* 2013, Zaveri *et al.* 2020), and thus it is not totally surprising that the genus *Rhynchobrunnera* had to be introduced to accommodate species that have 1–3-septate, straight conidia lacking apical beaks, in contrast to 1-septate conidia with hooked apical beaks in *Rhynchosporium* as delimited here. Furthermore, although *Rhynchosporium commune* was coined as a name for the barley scald pathogen (Zaffarano *et al.* 2011), Braun (2016) showed that *R. graminicola*, the type species of the genus, represented an older name for this taxon.



*Rhynchosporium commune* should thus be treated as synonym of *R. graminicola*.

Although species of *Oculimacula* (eyespot disease of cereals) have been well studied in the past (Nirenberg 1981), their generic circumscription (Crous *et al.* 2003) relied mainly on ribosomal gene phylogenies (ITS/LSU), which suggested four species to be accommodated in the genus. Of these, only two form typical *Oculimacula* apothecia, and are retained as *O. acuformis* and *O. yallundae*. *Helgardomyces* is introduced as a new genus based on *H. anguioides*, characterised by having fast-growing cultures with long, flexuous, subcylindrical, pluriseptate conidia, while *Pseudocercospora aestiva* is placed in *Cyphellophora*, based on its conidiogenous cells with flared phialides, which frequently develop directly on fungal hyphae.

Of all the genera treated here, *Spermospora* proved to be morphologically the most challenging, here segregated into two genera. *Neospermospora* *gen. nov.* is introduced for *S. avenae*, in addition to three new species of *Spermospora*, *S. arrhenatheri*, *S. loliiiphila* and *S. zaeae*. However, the species retained in *Spermospora* formed a paraphyletic group that warrants further studies, a matter that can only be resolved once fresh collections of the type species, *S. subulata* have been obtained.

Other genera that were considered either because they were phylogenetically related, or isolates were incorrectly identified under these names, include *Vanderaaea* and *Ypsilina*. *Ypsilina* (type: *Y. graminea*), occurs on various substrates, including roots and leaves of cereals, but appears to be of minor phytopathological importance. *Vanderaaea* *gen. nov.* (type: *V. ammophilae*), is a coelomycetous fungus occurring on dead leaves of *Ammophila arenaria*. Finally, the genus *Septogloeum*, which is a name that has been tentatively applied to some cereal fungi in the past, remains presently unresolved, pending further collections and acquisition of DNA data.

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**Conflict of interest:** The authors declare that there is no conflict of interest.

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**Supplementary Material:** <http://fuse-journal.org/>

**Fig. S1.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the ITS sequence alignment of sequences generated in this study and reference sequences from NCBI GenBank. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcoides* (culture NRRL 50072).

**Fig. S2.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the LSU sequence alignment of sequences generated in this study and reference sequences from NCBI GenBank. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcoides* (culture NRRL 50072).

**Fig. S3.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the *act* sequence alignment of sequences generated in this study and reference sequences from NCBI GenBank. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcoides* (culture NRRL 50072).



**Fig. S4.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the *rpb1* sequence alignment of sequences generated in this study and reference sequences from NCBI GenBank. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcooides* (culture NRRL 50072).

**Fig. S5.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the *rpb2* sequence alignment of sequences generated in this study and reference sequences from NCBI GenBank. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcooides* (culture NRRL 50072).

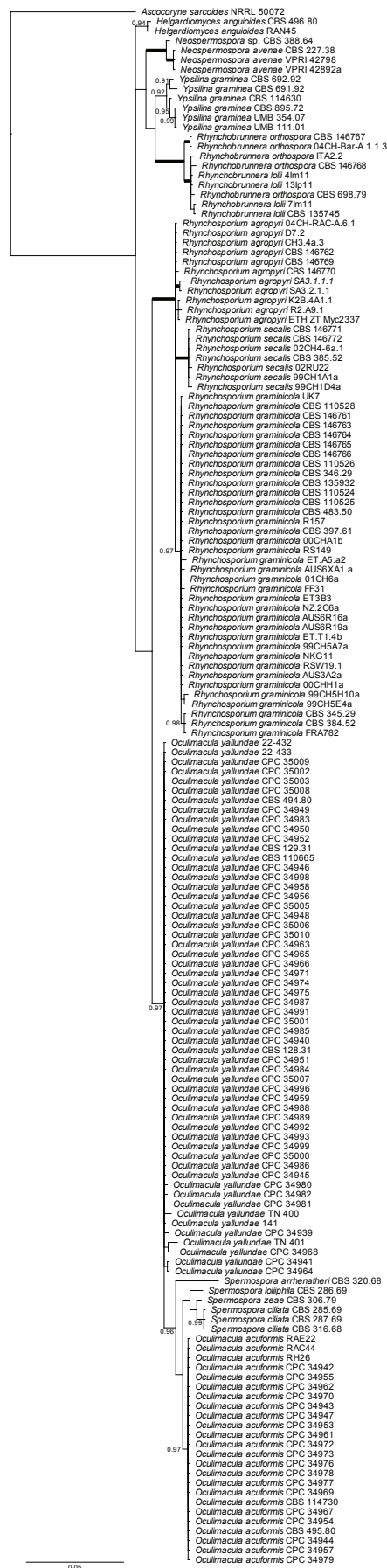
**Fig. S6.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the *tef1* sequence alignment of sequences generated in this study and reference sequences from NCBI GenBank. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcooides* (culture NRRL 50072).

**Fig. S7.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the full set 6-gene (ITS, LSU, *act*, *tef1*, *rpb1*, *rpb2*) sequence alignment. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcooides* (culture NRRL 50072).

**Fig. S8.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the full set 4-gene (ITS, LSU, *act*, *tef1*) sequence alignment. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcooides* (culture NRRL 50072).

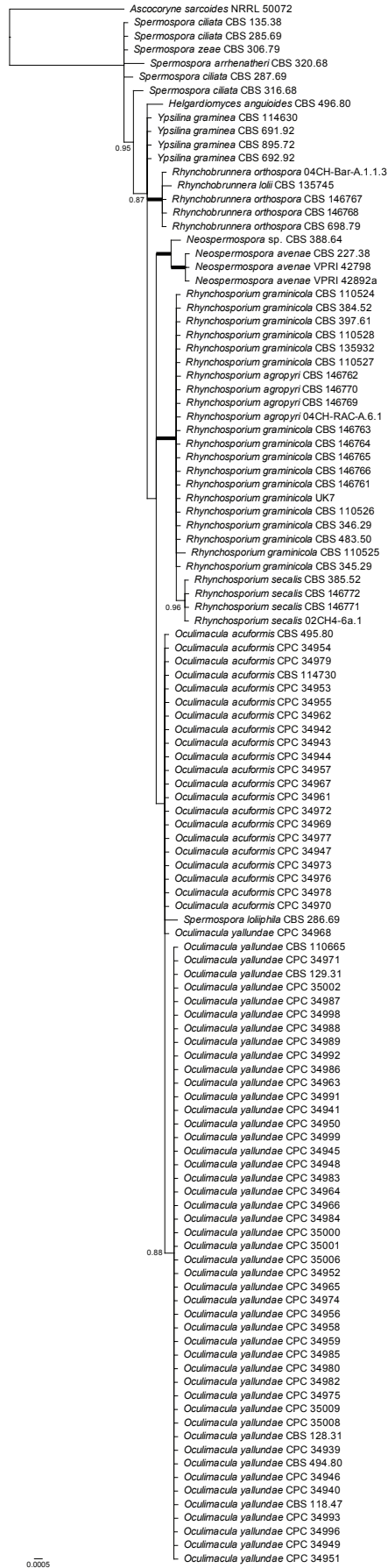
**Fig. S9.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the full set 2-gene (*rpb1*, *rpb2*) sequence alignment. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcooides* (culture NRRL 50072).

Figure S1



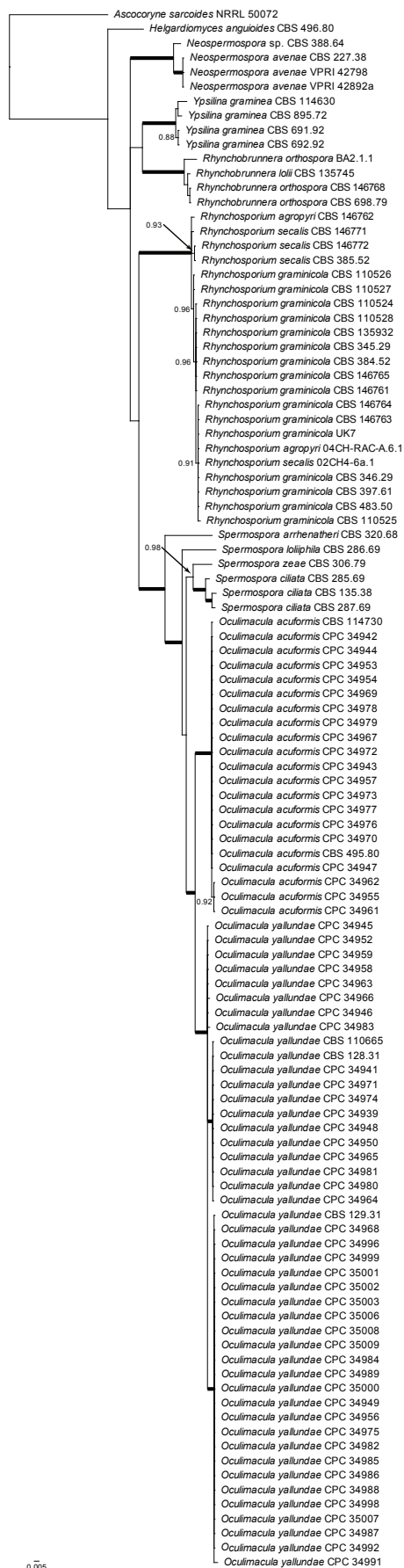
**Supplementary Fig 1.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the ITS sequence alignment of sequences generated in this study and reference sequences from NCBI GenBank. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascochyne sarcoides* (culture NRRL 50072).

Figure S2



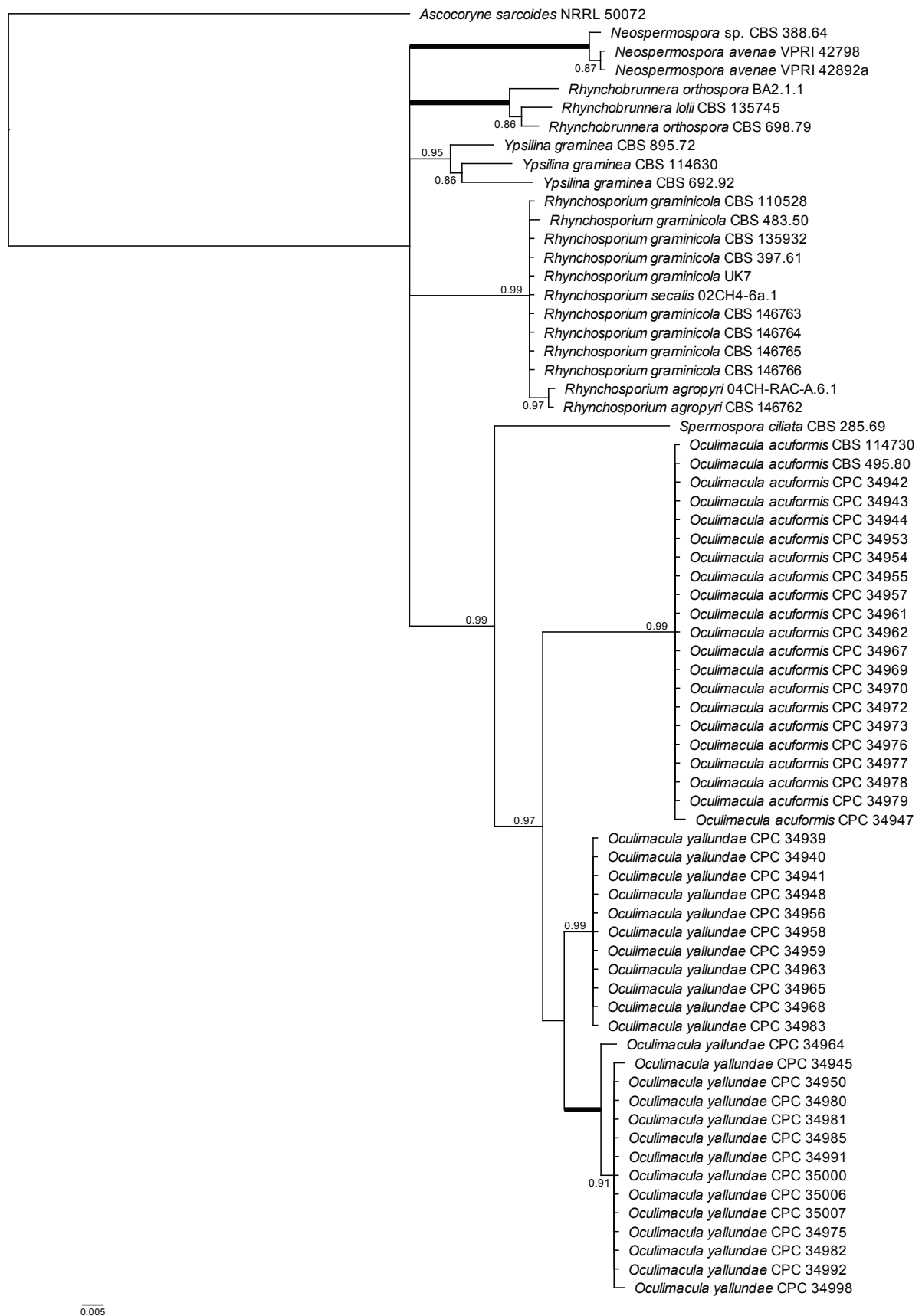
**Supplementary Fig 2.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the LSU sequence alignment of sequences generated in this study and reference sequences from NCBI GenBank. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcoides* (culture NRRL 50072).

Figure S3



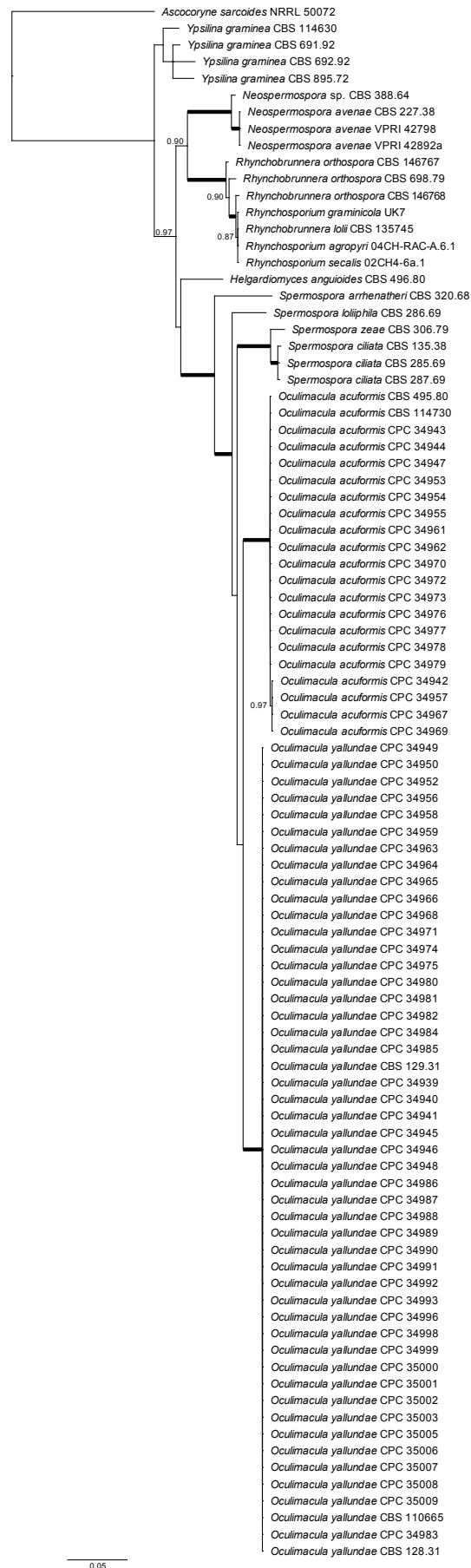
**Supplementary Fig 3.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the *act* sequence alignment of sequences generated in this study and reference sequences from NCBI GenBank. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcoides* (culture NRRL 50072).

Figure S4



**Supplementary Fig 4.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the *rbp1* sequence alignment of sequences generated in this study and reference sequences from NCBI GenBank. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcoides* (culture NRRL 50072).

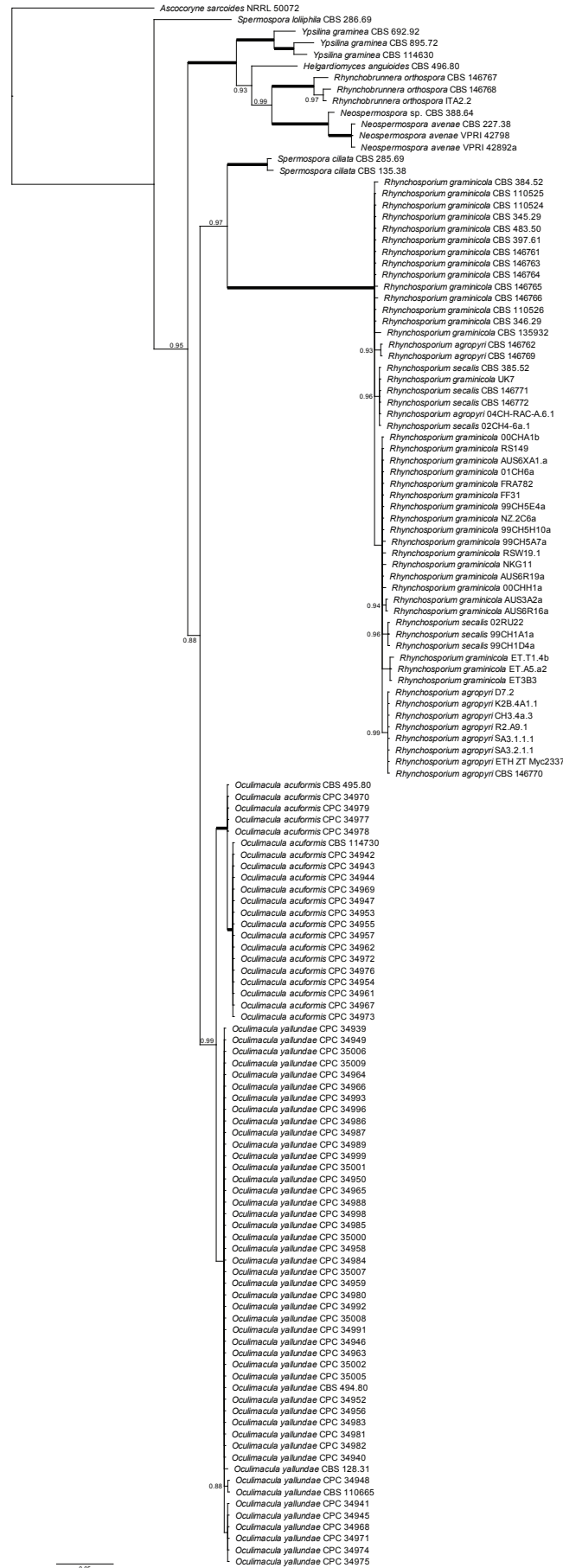
Figure S5



**Supplementary Fig 5.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the *rpb2* sequence alignment of sequences generated in this study and reference sequences from NCBI GenBank. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcoides* (culture NRRL 50072).



Figure S6



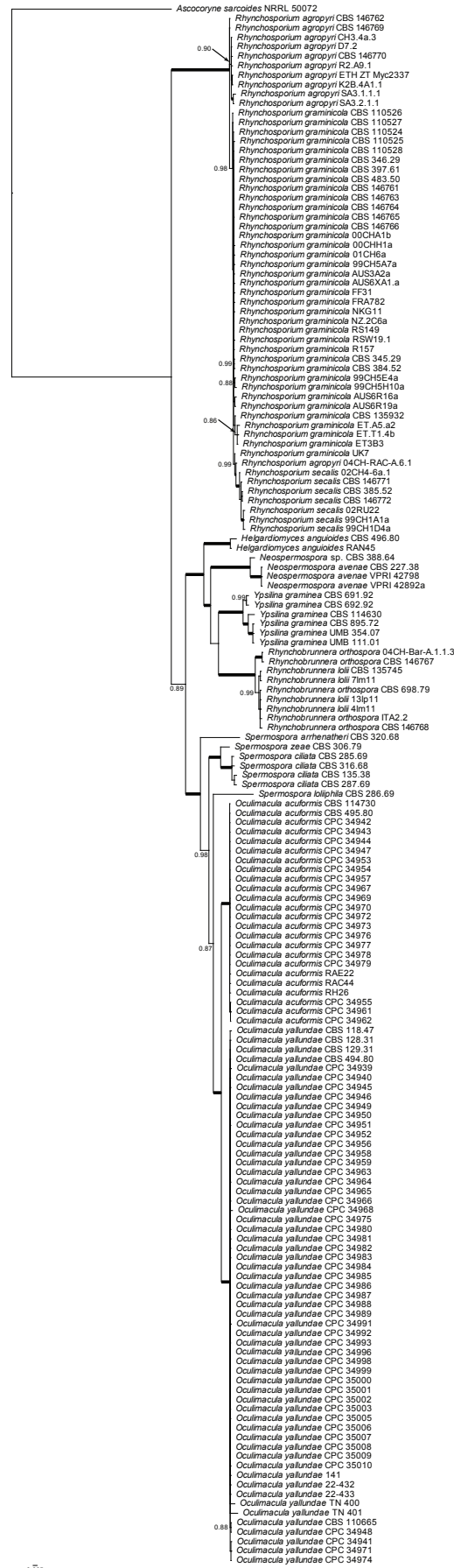
**Supplementary Fig 6.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the *tef1* sequence alignment of sequences generated in this study and reference sequences from NCBI GenBank. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascochyta sarcooides* (culture NRRL 50072).

Figure S7



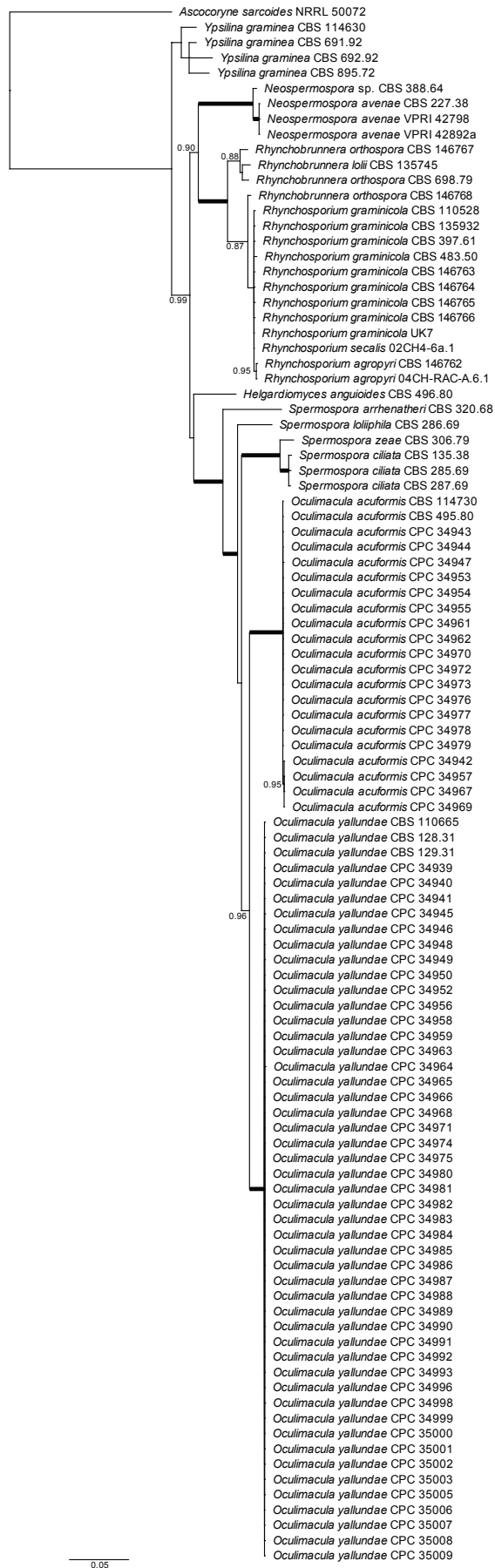
Supplementary Fig 7. Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the full set 6-gene (ITS, LSU, *act*, *tef1*, *rpb1*, *rpb2*) sequence alignment. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcoideae* (culture NRRL 50072).

Figure S8



**Supplementary Fig 8.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the full set 4-gene (ITS, LSU, *act*, *tef1*) sequence alignment. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcoides* (culture NRRL 50072).

Figure S9



**Supplementary Fig 9.** Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the full set 2-gene (*rpb1*, *rpb2*) sequence alignment. Bayesian posterior probabilities (PP) > 0.85 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species and culture collection numbers are indicated. The tree was rooted to *Ascocoryne sarcoides* (culture NRRL 50072).