

# The divorce of *Sporothrix* and *Ophiostoma*: solution to a problematic relationship

Z.W. de Beer<sup>1\*</sup>, T.A. Duong<sup>2</sup>, and M.J. Wingfield<sup>1</sup>

<sup>1</sup>Department of Microbiology and Plant Pathology, Forestry and Agricultural Research Institute (FABI), University of Pretoria, Pretoria 0002, South Africa; <sup>2</sup>Department of Genetics, Forestry and Agricultural Research Institute (FABI), University of Pretoria, Pretoria 0002, South Africa

\*Correspondence: Z.W. de Beer, [wilhelm.debeer@fabi.up.ac.za](mailto:wilhelm.debeer@fabi.up.ac.za)

**Abstract:** One of the causal agents of human sporotrichosis, *Sporothrix schenckii*, is the type species of the genus *Sporothrix*. During the course of the last century the asexual morphs of many *Ophiostoma* spp. have also been treated in *Sporothrix*. More recently several DNA-based studies have suggested that species of *Sporothrix* and *Ophiostoma* converge in what has become known as *Ophiostoma s. lat.* Were the one fungus one name principles adopted in the Melbourne Code to be applied to *Ophiostoma s. lat.*, *Sporothrix* would have priority over *Ophiostoma*, resulting in more than 100 new combinations. The consequence would be name changes for several economically important tree pathogens including *O. novo-ulmi*. Alternatively, *Ophiostoma* could be conserved against *Sporothrix*, but this would necessitate changing the names of the important human pathogens in the group. In this study, we sought to resolve the phylogenetic relationship between *Ophiostoma* and *Sporothrix*. DNA sequences were determined for the ribosomal large subunit and internal transcribed spacer regions, as well as the beta-tubulin and calmodulin genes in 65 isolates. The results revealed *Sporothrix* as a well-supported monophyletic lineage including 51 taxa, distinct from *Ophiostoma s. str.* To facilitate future studies exploring species level resolution within *Sporothrix*, we defined six species complexes in the genus. These include the *Pathogenic Clade* containing the four human pathogens, together with the *S. pallida*-, *S. candida*-, *S. inflata*-, *S. gossypina*- and *S. stenoceras* complexes, which include environmental species mostly from soil, hardwoods and *Protea* infructescences. The description of *Sporothrix* is emended to include sexual morphs, and 26 new combinations. Two new names are also provided for species previously treated as *Ophiostoma*.

**Key words:** *Sporothrix schenckii*, Sporotrichosis, Taxonomy, Nomenclature, One fungus one name.

**Taxonomic novelties: New combinations:** *Sporothrix abietina* (Marm. & Butin) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. aurorae* (X.D. Zhou & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. bragantina* (Pfenning & Oberw.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. candida* (Kamgan *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. cantabriensis* (P. Romón *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. dentifunda* (Aghayeva & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. epigloea* (Guerrero) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. eucalyptigena* (Barber & Crous) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. eucastaneae* (R.W. Davidson) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. euskadiensis* (P. Romón *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. fumea* (Kamgan *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. fusiformis* (Aghayeva & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. gemella* (Roets *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. gossypina* (R.W. Davidson) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. lunata* (Aghayeva & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. narcissi* (Limber) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. nebularis* (P. Romón *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. nigrograna* (Masuya) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. palmiculminata* (Roets *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. phasma* (Roets *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. polyporicola* (Constant & Ryman) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. prolifera* (Kowalski & Butin) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. protea-sedis* (Roets *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. stenoceras* (Robak) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. thermara* (J.A. van der Linde *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. zambiensis* (Roets *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf.; **New names:** *S. dombeyi* Z.W. de Beer, T.A. Duong & M.J. Wingf., *S. rossii* Z.W. de Beer, T.A. Duong & M.J. Wingf.

Available online 27 July 2016; <http://dx.doi.org/10.1016/j.simyco.2016.07.001>.

## INTRODUCTION

*Sporothrix* was established more than a century ago when Hektoen & Perkins (1900) presented a detailed case study of an American boy who contracted a fungal infection after wounding his finger with a hammer. They isolated and described the fungus, for which they provided the binomial *Sporothrix schenckii*. The epithet was derived from the name of B.R. Schenck, who described a similar fungus two years earlier, isolated from the infected wounds on an adult man (Schenck 1898). Schenck (1898) suggested that the fungus might be a species of *Sporotrichum*. However, Hektoen & Perkins (1900) applied the new genus name, *Sporothrix*, without providing an explicit generic diagnosis. The genus was thus considered invalid by most subsequent workers who referred to the fungus as *Sporotrichum schenckii* (De Beurmann & Gougerot 1911 and others). Carmichael (1962) stated that the fungus referred to by the earlier authors as *Sporotrichum schenckii*, did “not in the least resemble

*Sporotrichum aureum*”, the type species of the genus *Sporotrichum*, which was later shown to be a basidiomycete (Von Arx 1971, Stalpers 1978). He consequently relegated *Sporotrichum schenckii* back to *Sporothrix*, and did not consider it necessary to provide a Latin diagnosis for the genus (Carmichael 1962). Nicot & Mariat (1973) eventually validated the name with *S. schenckii* as type. de Hoog (1974) accepted their validation in his monograph of the genus, although Domsch *et al.* (1980) regarded the validation unnecessary “in view of the rather exhaustive *descriptio generico-specifica*” by Hektoen & Perkins (1900) [see Art. 38.5, McNeill *et al.* (2012)]. Nonetheless, the monograph of de Hoog (1974) provided the first thorough treatment in which 12 *Sporothrix* spp. were included and illustrated, together with the asexual states of 12 species of *Ophiostoma*.

The first connection between *Sporothrix* and *Ophiostoma* dates back more than a century, to Münch (1907) who treated the mycelial conidial states of some species of *Ophiostoma* (*Ceratostomella* at the time) in the genus *Sporotrichum*. The previous

year, [Hedgcock \(1906\)](#) described the synasexual morphs of some *Graphium* spp. also as *Sporotrichum*. Apart from *Sporotrichum*, both [Hedgcock \(1906\)](#) and [Münch \(1907\)](#) applied additional generic names, such as *Cephalosporium* and *Cladosporium*, to variations of the mycelial asexual morphs of *Ophiostoma*. Interestingly, most of the subsequent taxonomic treatments applied either *Cephalosporium* or *Cladosporium* when referring to the asexual morphs of *Ophiostoma* ([Lagerberg et al. 1927](#), [Melin & Nannfeldt 1934](#), [Siemaszko 1939](#), [Davidson 1942](#), [Bakshi 1950](#), [Mathiesen-Käärik 1953](#), [Hunt 1956](#)). Some authors applied other generic names to describe asexual morphs of *Ophiostoma*, such as *Cylindrocephalum*, *Hormodendron* ([Robak 1932](#)), *Hyalodendron* ([Goidanich 1935](#), [Georgescu et al. 1948](#)), and *Rhinotrichum* ([Georgescu et al. 1948](#), [Sczerbin-Parfenenko 1953](#)). [Barron \(1968\)](#) distinguished between *Sporothrix* and *Sporotrichum*, and suggested that the so-called *Sporotrichum* morphs described for some *Ceratocystis* (actually *Ophiostoma*) species should be referred to *Sporothrix*. In the same year, [Mariat & De Bievre \(1968\)](#) suggested that *Sporotrichum schenckii* was the asexual morph of a species of *Ceratocystis* (= *Ophiostoma*), later specified as *O. stenoceras* ([Andrieu et al. 1971](#), [Mariat 1971](#)).

[De Hoog's \(1974\)](#) monograph, in which he also listed *S. schenckii* as asexual morph of *O. stenoceras*, brought much needed order in the taxonomy of *Ophiostoma* asexual morphs. His circumscription of *Sporothrix* accommodated the plasticity of these species that had resulted in the above-mentioned confusion. He also appropriately included the asexual human pathogens in the same genus as the wood-staining fungi and bark beetle associates. Based on his work, many later authors treated asexual morphs previously ascribed to all the genera referred to above, in *Sporothrix* ([Samuels & Müller 1978](#), [Domsch et al. 1980](#), [Upadhyay 1981](#), [de Hoog 1993](#)). Several additional asexual species were also described in *Sporothrix* from a variety of hosts ([de Hoog 1978](#), [de Hoog & Constantinescu 1981](#), [Moustafa 1981](#), [de Hoog et al. 1985](#), [Constantinescu & Ryman 1989](#), and more). By the middle 1980's, evidence that *Sporothrix* is not a homogenous group, and that some of the species have basidiomycete affiliations, began to appear ([Smith & Batenburg-Van der Vegte 1985](#), [Weijman & de Hoog 1985](#), [de Hoog 1993](#)).

One of the earliest applications of DNA sequencing technology to resolve taxonomic questions in the fungal kingdom was published by [Berbee & Taylor \(1992\)](#). They used ribosomal small subunit (SSU) sequences to show that the asexual *S. schenckii* was phylogenetically related to the sexual genus *Ophiostoma*, represented in their trees by *O. ulmi* and *O. stenoceras*. This was the first study where DNA sequences were used to place an asexual fungus in a sexual genus. The following year, [Hausner et al. \(1993b\)](#) confirmed the separation of *Ceratocystis* and *Ophiostoma* based on ribosomal large subunit (LSU) sequences, and subsequently ([Hausner et al. 1993a](#)) published the first phylogeny of the genus *Ophiostoma*, showing that *Ophiostoma* spp. with *Sporothrix* asexual morphs do not form a monophyletic group within the *Ophiostomatales*. [Hausner et al. \(2000\)](#) produced a SSU phylogeny that included seven species in the *Ophiostomatales*. For the first time, *O. piliferum*, type species of *Ophiostoma*, together with *S. schenckii*, type species of *Sporothrix* were included together in a single phylogenetic tree. *Ophiostoma piliferum* grouped with *O. ips*, and *S. schenckii* formed a separate clade with *O. stenoceras*.

In the two decades subsequent to the first DNA-based phylogeny ([Berbee & Taylor 1992](#)), increasing numbers of taxa were included in *Ophiostoma* phylogenies. In these studies, the separation between *Ophiostoma s. str.* and what became known as the *S. schenckii*–*O. stenoceras* complex, became more apparent ([De Beer et al. 2003](#), [Villarreal et al. 2005](#), [Roets et al. 2006](#), [Zipfel et al. 2006](#), [De Meyer et al. 2008](#), [Linnakoski et al. 2010](#), [Kamgan Nkuekam et al. 2012](#)). This was also evident in the most comprehensive phylogenies of the *Ophiostomatales* to date that included 266 taxa ([De Beer & Wingfield 2013](#)). These authors treated the *S. schenckii*–*O. stenoceras* complex, including 26 taxa producing only sporothrix-like asexual states, in *Ophiostoma sensu lato*. They excluded the complex from *Ophiostoma sensu stricto*, which contained several other species with sporothrix-like asexual states, often in combination with synnematus, pesotum-like asexual states.

The capacity to link sexual and asexual species and genera based on DNA sequences, as exhibited by the [Berbee & Taylor \(1992\)](#) study, had a major impact on fungal taxonomy and nomenclature. The long-standing debate regarding the impracticality of a dual nomenclature system culminated in the adoption of a single-name nomenclatural system for all fungi in the newly named International Code of Nomenclature for algae, fungi, and plants (ICN) at the 2011 International Botanical Congress in Melbourne, Australia. Only one name for a single fungus has been allowed after 1 January 2013 ([Hawksworth 2011](#), [Norvell 2011](#)). This means that all names for a single taxon now compete equally for priority, irrespective of the morph that they represent ([Hawksworth 2011](#)). If these rules were to be applied indiscriminately and with immediate effect, the taxonomic impacts on the *Ophiostomatales* would be immense ([De Beer & Wingfield 2013](#)) and frustrating to practitioners such as plant pathologists and medical mycologists ([Wingfield et al. 2012](#)).

*Ophiostoma s. lat.* as defined by [De Beer & Wingfield \(2013\)](#) included the *O. ulmi*-, *O. pluriannulatum*-, *O. ips*-, and *S. schenckii*–*O. stenoceras* complexes, as well as *O. piliferum* and more than 20 other *Ophiostoma* spp. The new rules dictate that *Sporothrix* as the older name would have priority over *Ophiostoma* ([Hektoen & Perkins 1900](#), [Sydow and Sydow 1919](#)). The result would be a redefined *Sporothrix* containing more than 150 species, 112 of which would require new combinations, including well-known tree pathogens such as the Dutch elm disease fungi, *O. ulmi* and *O. novo-ulmi*. Alternatively, the ICN makes provision for the conservation of a younger, better known genus name against an older, lesser known name (Article 14, [McNeill et al. 2012](#)). If *Ophiostoma* were to be conserved against *Sporothrix*, it would have resulted in only 22 new combinations in *Ophiostoma*, but with changed names for all the major causal agents of the important human and animal disease sporotrichosis: *S. schenckii*, *S. brasiliensis* and *S. globosa*. Based on a lack of DNA sequence data for a number of *Sporothrix* spp. at the time, and to avoid nomenclatural chaos, [De Beer & Wingfield \(2013\)](#) made several recommendations that ensured nomenclatural stability for the *Ophiostomatales*, for the interim and before alternative taxonomic solutions could be found. One of these recommendations was to reconsider the generic status of species complexes such as the *S. schenckii*–*O. stenoceras* complex.

During the past decade, sequence data for several gene regions have been employed to delineate closely related species in the *S. schenckii*–*O. stenoceras* complex. A difficulty encountered has been that medical mycologists working with *S. schenckii* and the other human- and animal-pathogenic

species, have used gene regions to distinguish between cryptic species that differ from those used by plant pathologists and generalist mycologists. The latter group have primarily used sequences for the internal transcribed spacer region (ITS) (De Beer *et al.* 2003, Villarreal *et al.* 2005) or the beta-tubulin (*BT*) gene (Aghayeva *et al.* 2004, 2005, Roets *et al.* 2006, 2008, 2010, Zhou *et al.* 2006, De Meyer *et al.* 2008, Kamgan Nkuekam *et al.* 2008, 2012, Linnakoski *et al.* 2008, 2010, Madrid *et al.* 2010a). In contrast, medical mycologists have experimented with several gene regions, still including ITS (Gutierrez Galhardo *et al.* 2008, Zhou *et al.* 2014) and *BT*, but also including chitin synthase, calmodulin (*CAL*) (Marimon *et al.* 2006, 2008), and most recently translation elongation factor-1-alpha (*TEF1*) and translation elongation factor-3 (*TEF3*) (Zhang *et al.* 2015, Rodrigues *et al.* 2016). *CAL* became the preferred gene region to distinguish among the human pathogenic species of *Sporothrix* (Marimon *et al.* 2007, Madrid *et al.* 2009, Dias *et al.* 2011, Oliveira *et al.* 2011, Romeo *et al.* 2011, Rodrigues *et al.* 2014b, 2015a, 2015b, 2016). A potential problem that could arise from this history is that environmental isolates included in clinical studies could be incorrectly identified because at present, no *CAL* sequences are available for many of the non-pathogenic species in *S. schenckii*–*O. stenoceras* complex which are mostly from wood, soil and *Protea* infructescences.

The aims of this study were 1) to redefine the genus *Sporothrix*, 2) to provide new combinations where necessary, 3) to provide sequence data for ex-type isolates of as many species as possible in the emended genus, so that reference sequences will be available for future taxonomic and clinical studies, and 4) to define emerging species complexes within *Sporothrix*. To address the genus level questions we employed the ribosomal LSU and ITS regions. Species level questions were addressed using the ITS regions, widely accepted as the universal DNA barcode marker for fungi (Schoch *et al.* 2012), as well as sequences for the more variable protein-coding *CAL* and *BT* genes.

## MATERIALS & METHODS

### Isolates

Forty three *Ophiostoma*, two *Ceratocystis* and one *Dolichoascus* species, all with sporothrix-like asexual morphs, were considered in our study, together with 27 *Sporothrix* spp. without known sexual morphs (Table 1). The total number of 73 species were represented by DNA sequences of 83 isolates, as more than one isolate was included for some of the species. Sixty six of the isolates are linked to type specimens, and sequences of 18 isolates generated in previous studies were obtained from GenBank.

### DNA extraction, PCR and DNA sequencing

DNA was extracted following the technique described by Duong *et al.* (2012). The ribosomal LSU region was amplified and sequenced using primers LR3 and LR5 (White *et al.* 1990), while ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990) were used for the ITS regions. The PCR reactions of the *BT* genes were run using primers T10 (O'Donnell & Cigelnik 1997) and Bt2b, while Bt2a and Bt2b (Glass & Donaldson 1995) were used for sequencing reactions. For the *CAL* gene, primers CL1 and CL2a (O'Donnell *et al.* 2000) were used for most species, but a new

primer pair was designed for some *Ophiostoma* spp. that could not be amplified with these primers. The new primers were CL3F (5'-CCGARTWCAAGGAGGCSTTC-3') and CL3R (5'-TTCTGCAT-CATRAGYTGSAC-3'). PCR and sequencing protocols were as described by Duong *et al.* (2012), other than the annealing temperature being optimized for some individual reactions.

### Phylogenetic analyses

Data sets of sequences derived in the present study (Table 1) together with reference sequences obtained from NCBI GenBank, were compiled using MEGA 6.06 (Tamura *et al.* 2013). All datasets (LSU, ITS, *BT* and *CAL*) were aligned using an online version of MAFFT 7 (Kato & Standley 2013) and subjected to Gblocks 0.91b (Castresana 2000) using less stringent selection options, to eliminate poorly aligned positions and divergent regions from subsequent phylogenetic analyses. All datasets obtained from Gblocks were subjected to Maximum Likelihood (ML) and Bayesian Inference (BI) analyses. ML analyses using RaxML (Stamatakis 2006) were conducted with raxmlGUI 1.3 (Silvestro & Michalak 2012) with 10 runs using the GTRGAMMA substitution model and 1 000 bootstraps each. BI analyses were conducted with MrBayes 3.2.5 (Ronquist & Huelsenbeck 2003) with 10 runs using the GTRGAMMA substitution model, and 5 M generations each with tree sampling every 100<sup>th</sup> generation. Bayesian posterior probabilities were calculated for each dataset after discarding 25% of the trees sampled as prior burn-in.

## RESULTS

### Phylogenetic analyses

Trees obtained from MrBayes analyses with support values for branches are presented in Fig. 1 (LSU), Fig. 2 (ITS), Fig. 3 (*BT*) and Fig. 4 (*CAL*). The numbers of taxa and characters included in the respective data sets, as well as outgroups, are presented in the legends of Figs 1–4. Topologies of trees obtained from ML analyses were largely congruent with the MrBayes trees and bootstrap support values for these are also indicated in the figures.

The LSU data (Fig. 1) showed well-supported lineages for the following genera (as defined by De Beer & Wingfield 2013) in the *Ophiostomatales*: *Leptographium* s. lat., *Ophiostoma* s. str., *Fragosphaeria*, *Ceratocystiopsis*, *Raffaella* s. str., and *Graphilbum*. Two genera described subsequent to the study of De Beer & Wingfield (2013) were also supported in the LSU analyses, namely *Aureovirgo* (Van der Linde *et al.* 2016) and *Hawksworthiomyces* (De Beer *et al.* 2016). The *S. schenckii*–*O. stenoceras* complex as defined by De Beer & Wingfield (2013), formed a well-supported lineage distinct from *Ophiostoma* s. str. This lineage included *Sporothrix schenckii*, the type species of *Sporothrix*, and was thus labelled as *Sporothrix*. It also included 16 other known *Sporothrix* spp., 29 known *Ophiostoma* spp., the ex-type isolates of *Ceratocystis gossypina* var. *robusta* and *C. eucastanea*, and a novel taxon labelled as 'S. curviconia 2', that was previously identified as that species. One *Sporothrix* species, *S. nothofagi*, did not group in *Sporothrix*, but in a distinct lineage within *Leptographium* s. lat. Several species with sporothrix-like asexual morphs grouped in *Ophiostoma* s. str. and are listed in the Taxonomy section below. However, some *Ophiostoma* spp. with sporothrix-like asexual



**Table 1.** Isolates of species with sporothrix-like asexual states included in phylogenetic analyses in this study. Genbank numbers for sequences obtained in the present study are printed in bold type.

Previous name	New name	CMW <sup>1</sup>	CBS <sup>2</sup> or other	Type	Isolated from	Country	Collector	GenBank Accession numbers			
								LSU	ITS	BT	CAL
<i>Ceratocystis eucastanea</i>	<i>S. eucastanea</i>	1124	424.77	T	canker on <i>Castanea dentata</i>	North Carolina, USA	RW Davidson	<b>KX590843</b>	<b>KX590814</b>	<b>KX590753</b>	<b>KX590781</b>
<i>C. gossypina</i> var. <i>robusta</i>	<i>S. rossii</i>	1118	116.78	T	<i>Dendroctonus adjunctus</i> gallery on <i>P. ponderosa</i>	New Mexico, USA	RW Davidson	<b>KX590844</b>	<b>KX590815</b>	<b>KX590754</b>	JQ511972
<i>Dolichoascus schenckii</i>	syn. <i>S. schenckii</i>		938.72	T	Human	France	F Mariat	NA	KP017094	NA	AM490340
<i>O. abietinum</i>	<i>S. abietina</i>	22310	125.89	T	<i>Pseudohylesinus</i> gallery on <i>Abies vejari</i>	Mexico	JG Marmolejo	<b>KX590845</b>	AF484453	<b>KX590755</b>	JQ511966
<i>O. africanum</i>	<i>S. africana</i>	823	116571		<i>Protea gaguedi</i>	South Africa	MJ Wingfield	DQ316147	DQ316199	DQ296073	NA
<i>O. albidum</i>	syn. <i>S. stenoceras</i>	1123	798.73	T	<i>Pissodes pini</i> gallery on <i>Pinus sylvestris</i>	Sweden	A Mathiesen-Käärik	<b>KX590846</b>	AF484475	<b>KX590756</b>	<b>KX590782</b>
<i>O. angusticollis</i>	<i>O. angusticollis</i>	152	186.86		<i>Pinus banksiana</i>	Wisconsin, USA	MJ Wingfield	<b>KX590847</b>	AY924383*	<b>KX590757*</b>	NA
<i>O. aurorae</i>	<i>S. aurorae</i>	19362	118837	T	<i>Hylastes angustatus</i> on <i>Pinus elliotii</i>	South Africa	XD Zhou	<b>KX590848</b>	DQ396796	DQ396800	<b>KX590783</b>
<i>O. braganinum</i>	<i>S. braganina</i>	17149	474.91	T	Virgin forest soil	Brazil	W Gams	<b>KX590849</b>	FN546965	FN547387	<b>KX590784</b>
<i>O. candidum</i>	<i>S. candida</i>	26484	129713	T	<i>Eucalyptus cloeziana</i>	South Africa	G Kamgan Nkuekam	<b>KX590850</b>	HM051409	HM041874	<b>KX590785</b>
<i>O. cantabriense</i>	<i>S. cantabriensis</i>	39766	136529	T	<i>Hylastes attenuates</i> on <i>Pinus sylvestris</i>	Spain	P Romon	NA	KF951554	KF951544	KF951540
<i>O. coronatum</i>	<i>O. coronatum</i>	37433	497.77			Canada	RW Davidson	<b>KX590851</b>	AY924385*	<b>KX590758*</b>	<b>KX590786*</b>
<i>O. denticulatum</i>	<i>O. denticulatum</i>	1128	ATCC38087	T	Ambrosia gallery <i>Pinus ponderosa</i>	Colorado, USA	RW Davidson	<b>KX590852</b>	<b>KX590816*</b>	<b>KX590759*</b>	NA
<i>O. dentifundum</i>	<i>S. dentifunda</i>	13016	115790	T	<i>Quercus</i> wood	Hungary	C Delatour	<b>KX590853</b>	AY495434	AY495445	<b>KX590787</b>
<i>O. epigloeum</i>	<i>S. epigloea</i>	22308	573.63	T	<i>Tremella fusiformis</i>	Argentina	RT Guerrero	<b>KX590854</b>	<b>KX590817</b>	<b>KX590760</b>	NA
<i>O. eucalyptigena</i>	<i>S. eucalyptigena</i>		139899	T	<i>Eucalyptus marginata</i>	Australia	PA Barber	KR476756	KR476721	NA	NA
<i>O. euskadiense</i>	<i>S. euskadiensis</i>	27318	122138	T	<i>Hylurgops palliatus</i> on <i>Pinus radiata</i>	Spain	XD Zhou	NA	DQ674369	EF396344	JQ438830
<i>O. fumeum</i>	<i>S. fumea</i>	26813	129712	T	<i>Eucalyptus cloeziana</i>	South Africa	G Kamgan Nkuekam, J Roux	NA	HM051412	HM041878	<b>KX590788</b>
		26820			<i>Eucalyptus</i> sp.	Zambia	G Kamgan Nkuekam	<b>KX590855</b>	<b>KX590818</b>	NA	NA
<i>O. fusiforme</i>	<i>S. fusiformis</i>	9968	112912	T	<i>Populus nigra</i>	Azerbaijan	D Aghayeva	DQ294354	AY280481	AY280461	JQ511967
<i>O. gemellus</i>	<i>S. gemella</i>	23057	121959	T	<i>Tarsonemus</i> sp. from <i>Protea caffra</i>	South Africa	F Roets	DQ821531	DQ821560	DQ821554	NA
<i>O. gossypinum</i>	<i>S. gossypina</i>	1116	ATCC18999	T	<i>P. ponderosa</i>	New Mexico, USA	RW Davidson	<b>KX590856</b>	<b>KX590819</b>	<b>KX590761</b>	<b>KX590789</b>
<i>O. grande</i>	<i>O. grande</i>	22307	350.78	T	<i>Diatrype</i> fruiting body on bark	Brazil	RD Dumont	<b>KX590857</b>	NA	NA	<b>KX590790</b>
<i>O. grandicarpum</i>	<i>O. grandicarpum</i>	1600	250.88	T	<i>Quercus robur</i>	Poland	T Kowalski	<b>KX590858</b>	<b>KX590820*</b>	<b>KX590762*</b>	NA
<i>O. lunatum</i>	<i>S. lunata</i>	10563	112927	T	<i>Carpinus betulus</i>	Austria	T Kirisits	<b>KX590859</b>	AY280485	AY280466	JQ511970
<i>O. macrosporum</i>	<i>O. macrosporum</i>	14176	367.53		<i>Ips acuminatus</i>	Sweden	H Francke-Grosmann	EU177468	<b>KX590821*</b>	<b>KX590763*</b>	NA
<i>O. microsporum</i>	<i>O. microsporum</i>	17152	440.69	NT	<i>Quercus</i> sp.	Virginia, USA	EG Kuhlman	<b>KX590860</b>	<b>KX590822*</b>	<b>KX590764*</b>	NA
<i>O. narcissi</i>	<i>S. narcissi</i>	22311	138.50	T	<i>Narcissus</i> sp.	Netherlands	DP Limber	<b>KX590861</b>	AF194510	<b>KX590765</b>	<b>KX590791</b>
<i>O. nebulare</i>	<i>S. nebularis</i>	22797			<i>Orthotomicus erosus</i> on <i>Pinus radiata</i>	Spain	P Romon	<b>KX590862</b>	<b>KX590823</b>	NA	JQ438829
		27319	122135	T	<i>Hylastes attenuatus</i> on <i>Pinus radiata</i>	Spain	P Romon	NA	<b>KX590824</b>	<b>KX590766</b>	JQ438828
<i>O. nigricarpum</i>	<i>O. nigricarpum</i>	651	638.66	P	<i>Pseudotsuga menziesii</i>	Idaho, USA	RW Davidson	DQ294356	AY280490*	AY280480*	NA

Table 1. (Continued)

Previous name	New name	CMW <sup>1</sup>	CBS <sup>2</sup> or other	Type	Isolated from	Country	Collector	GenBank Accession numbers			
								LSU	ITS	BT	CAL
<i>O. nigricarpum</i>	<i>O. nigricarpum</i>	650	637.66	T	<i>Abies</i> sp.	Idaho, USA	RW Davidson	NA	AY280489*	AY280479*	NA
<i>O. nigrogranum</i>	<i>S. nigrograna</i>	14487	MAFF410943	T	<i>Pinus densiflora</i>	Japan	H Masuya	<b>KX590863</b>	<b>KX590825</b>	NA	NA
<i>O. noisomeae</i>	<i>O. noisomeae</i>	40326	141065	T	<i>Rapanea melanophloeos</i>	South Africa	T Musvuugwa	<b>KX590864</b>	KU639631	KU639628	<b>KX590792</b>
		40329	141066	P	<i>Rapanea melanophloeos</i>	South Africa	T Musvuugwa	NA	KU639634	KU639630	KU639611
<i>O. nothofagi</i>	<i>S. dombeyi</i>	1023	455.83	T	<i>Nothofagus dombeyi</i>	Chile	H Butin	<b>KX590865</b>	<b>KX590826</b>	<b>KX590767</b>	<b>KX590793</b>
<i>O. palmiculminatum</i>	<i>S. palmiculminata</i>	20677	119590	T	<i>Protea repens</i>	South Africa	F Roets	DQ316143	DQ316191	DQ316153	<b>KX590794</b>
<i>O. phasma</i>	<i>S. phasma</i>	20676	119721	T	<i>Protea laurifolia</i>	South Africa	F Roets	DQ316151	DQ316219	DQ316181	<b>KX590795</b>
<i>O. polyporicola</i>	<i>S. polyporicola</i>	5461	669.88	T	<i>Fomitopsis pinicola</i>	Sweden	S Ryman	<b>KX590866</b>	<b>KX590827</b>	<b>KX590768</b>	<b>KX590796</b>
<i>O. ponderosae</i>	<i>O. ponderosae</i>	37953	ATCC26665	T	<i>P. ponderosa</i>	Arizona, USA	TE Hinds	<b>KX590867</b>	NA	NA	NA
<i>O. ponderosae</i>	' <i>O. ponderosae</i> 2'	128	RWD899		Not known	USA	TE Hinds	<b>KX590868</b>	<b>KX590828*</b>	<b>KX590769*</b>	NA
<i>O. proliferum</i>	<i>S. prolifera</i>	37435	251.88	T	<i>Quercus robur</i>	Poland	T Kowalski	<b>KX590869</b>	<b>KX590829</b>	<b>KX590770</b>	<b>KX590797</b>
<i>O. protearum</i>	<i>S. protearum</i>	1107	116654		<i>P. caffra</i>	South Africa	MJ Wingfield	DQ316145	DQ316201	DQ316163	<b>KX590798</b>
<i>O. protea-sedis</i>	<i>S. protea-sedis</i>	28601	124910	T	<i>P. caffra</i>	Zambia	F Roets	<b>KX590870</b>	EU660449	EU660464	NA
<i>O. rostrocoronatum</i>	<i>O. rostrocoronatum</i>	456	434.77		Pulpwood chips of hardwoods	Colorado, USA	RW Davidson	<b>KX590871</b>	AY194509*	<b>KX590771*</b>	NA
<i>O. splendens</i>	<i>S. splendens</i>	897	116379		<i>Protea repens</i>	South Africa	F Roets	AF221013	DQ316205	DQ316169	<b>KX590799</b>
<i>O. stenoceras</i>	<i>S. stenoceras</i>	3202	237.32	T	Pine pulp	Norway	H Robak	DQ294350	AY484462	DQ296074	JQ511956
<i>O. tenellum</i>	<i>O. tenellum</i>	37439	189.86		<i>Pinus banksiana</i>	Wisconsin, USA	MJ Wingfield	<b>KX590872</b>	AY934523*	<b>KX590772*</b>	<b>KX590800*</b>
<i>O. thermarum</i>	<i>S. thermara</i>	38930	139747	T	<i>Cyrtogenius africanus</i> galleries on <i>Euphorbia ingens</i>	South Africa	JA van der Linde	KR051127	KR051115	KR051103	NA
<i>O. valdivianum</i>	<i>O. valdivianum</i>	449	454.83	T	<i>Nothofagus alpina</i>	Chile	H Butin, M Osorio	<b>KX590873</b>	<b>KX590830</b>	<b>KX590773</b>	<b>KX590801</b>
<i>O. zambiensis</i>	<i>S. zambiensis</i>	28604	124912	T	<i>Protea caffra</i>	Zambia	F Roets	<b>KX590874</b>	EU660453	EU660473	NA
<i>Sporotrichum tropicale</i> nom. inval.	syn. <i>S. globosa</i>	17204	292.55	T	Human	India	LM Gosh	<b>KX590875</b>	KP017086	<b>KX590774</b>	AM490354
<i>Sporothrix aemulophila</i>	<i>S. aemulophila</i>	40381	140087	T	<i>Rapanea melanophloeos</i>	South Africa	T Musvuugwa	NA	KT192603	KT192607	<b>KX590802</b>
<i>S. albicans</i>	syn. <i>S. pallida</i>	17203	302.73	T	Soil	England	SB Saksena	<b>KX590876</b>	<b>KX590831</b>	AM498343	AM398396
<i>S. brasiliensis</i>	<i>S. brasiliensis</i>	29127	120339	T	Human skin	Brazil	M dos Santos Lazéra	<b>KX590877</b>	<b>KX590832</b>	AM116946	AM116899
<i>S. brunneoviolacea</i>	<i>S. brunneoviolacea</i>	37443	124561	T	Soil	Spain	H Madrid	<b>KX590878</b>	FN546959	FN547385	<b>KX590803</b>
<i>S. cabralii</i>	<i>S. cabralii</i>	38098	CIEFAP456	T	<i>Nothofagus pumilio</i>	Argentina	A de Errasti	KT362229	KT362256	KT381295	<b>KX590804</b>
<i>S. catenata</i>	<i>Trichomonascus ciferii</i>	17161	215.79	T	Calf skin	Romania	O Constantinescu	<b>KX590879*</b>	<b>KX590833*</b>	NA	NA
<i>S. catenata</i>	<i>S. pallida</i>	17162	461.81		Nail of man	Netherlands	GS de Hoog	NA	<b>KX590834</b>	<b>KX590775</b>	<b>KX590805</b>
<i>S. chilensis</i>	<i>S. chilensis</i>		139891	T	Human	Chile	R Cruz Choappa	NA	KP711811	KP711813	KP711815
<i>S. curviconia</i>	<i>S. curviconia</i>	17164	959.73	T	<i>Terminalia ivorensis</i>	Ivory Coast	J Devois	<b>KX590880</b>	<b>KX590835</b>	<b>KX590776</b>	NA

(continued on next page)

Table 1. (Continued)

Previous name	New name	CMW <sup>1</sup>	CBS <sup>2</sup> or other	Type	Isolated from	Country	Collector	GenBank Accession numbers			
								LSU	ITS	BT	CAL
<i>S. curviconia</i>	' <i>S. curviconia</i> 2'	17163	541.84		<i>Pinus radiata</i> log	Chile	HL Peredo	<b>KX590881</b>	<b>KX590836</b>	<b>KX590777</b>	JQ511968
<i>S. dimorphospora</i>	<i>S. dimorphospora</i>	12529	553.74	T	Soil	Canada	RAA Morall	NA	AY495428	AY495439	NA
		37446	125442		Soil	Spain	C Silverra	<b>KX590882</b>	FN546961	FN547379	<b>KX590806</b>
<i>S. fungorum</i>	Uncertain	17165	259.70	T	<i>Fomes fomentarius</i> basidiome	Germany	W Gams	<b>KX590883*</b>	<b>KX590837*</b>	NA	NA
<i>S. globosa</i>	<i>S. globosa</i>	29128	120340	T	Human face	Spain	C Rubio	<b>KX590884</b>	<b>KX590838</b>	AM116966	AM166908
<i>S. guttuliformis</i>	<i>S. guttuliformis</i>	17167	437.76	T	Soil	Malaysia	T Furukawa	<b>KX590885</b>	<b>KX590839</b>	<b>KX590778</b>	<b>KX590807</b>
<i>S. humicola</i>	<i>S. humicola</i>	7618	118129	T	Soil	South Africa	HF Vismer	EF139114	AF484472	EF139100	<b>KX590808</b>
<i>S. inflata</i>	' <i>S. inflata</i> 2'	12526	156.72		Greenhouse soil	Netherlands	H Kaastra-Howeler	NA	AY495425	AY495436	NA
<i>S. inflata</i>	<i>S. inflata</i>	12527	239.68	T	Wheat field soil	Germany	W Gams	DQ294351	AY495426	AY495437	NA
<i>S. itsvo</i>	<i>S. itsvo</i>	40370	141063	T	<i>Rapanea melanophloeos</i>	South Africa	T Musvuugwa	NA	<b>KX590840</b>	KU639625	NA
<i>S. lignivora</i>	<i>Hawksworthiomyces lignivora</i>	18600	119148	T	<i>Eucalyptus</i> utility poles	South Africa	EM de Meyer	EF139119	EF127890*	EF139104*	NA
		18599	119147		<i>Eucalyptus</i> utility poles	South Africa	EM de Meyer	KX396545	EF127889*	EF139103*	NA
<i>S. luriei</i>	<i>S. luriei</i>	17210	937.72	T	Human skin	South Africa	H Lurie	<b>KX590886</b>	AB128012	AM747289	AM747302
<i>S. mexicana</i>	<i>S. mexicana</i>	29129	120341	T	Soil, rose tree	Mexico	A Espinosa	<b>KX590887</b>	<b>KX590841</b>	AM498344	AM398393
<i>S. nivea</i>	syn. <i>S. pallida</i>	17168	150.87	T	Sediment in water purification plant	Germany	G Teuscher, F Schauer	<b>KX590888</b>	EF127879	<b>KX590779</b>	<b>KX590809</b>
<i>S. nothofagi</i>	<i>S. nothofagi</i>	37658	NZFS519	T	<i>Nothofagus fusca</i>	New Zealand	W Faulds	<b>KX590889</b>	NA	<b>KX590780*</b>	<b>KX590810*</b>
<i>S. pallida</i>	<i>S. pallida</i>	17209	131.56	T	<i>Stemonitis fusca</i>	Japan	K Tubaki	EF139121	EF127880	EF139110	<b>KX590811</b>
<i>S. rapaneae</i>	<i>S. rapaneae</i>	40369	141060	T	<i>Rapanea melanophloeos</i>	South Africa	T Musvuugwa	NA	KU595583	KU639624	KU639609
<i>S. schenckii</i>	<i>S. schenckii</i>	29351	359.36	T	Human	USA	CF Perkins	<b>KX590890</b>	<b>KX590842</b>	AM116911	AM117437
<i>S. stylites</i>	<i>S. stylites</i>	14543	118848	T	Pine utility poles	South Africa	EM de Meyer	EF139115	EF127883	EF139096	<b>KX590812</b>
<i>S. uta</i>	<i>S. uta</i>	40316	141069	P	<i>Rapanea melanophloeos</i>	South Africa	T Musvuugwa	NA	KU595577	KU639616	KU639605
<i>S. variecibatus</i>	<i>S. variecibatus</i>	23051	121961	T	<i>Trichouropoda</i> sp. from <i>Protea repens</i>	South Africa	F Roets	DQ821537	DQ821568	DQ821539	<b>KX590813</b>

T = ex-type; NT = ex-neotype; P = ex-paratype.

\*Sequences not included in ITS, BT and CAL analyses of the present study because sequences were too divergent.

<sup>1</sup> CMW = Culture Collection of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa.

<sup>2</sup> CBS = Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; ATCC = American Type Culture Collection, Manassas, VA, USA; MAFF = Ministry of Agriculture, Forestry, and Fisheries, Genetic Resource Centre, Culture Collection of National Institute of Agrobiological Resources, Japan; RWD = Private collection of R.W. Davidson; CIEFAP = Culture collection of the Centro de Investigación y Extensión Forestal Andino Patagónico, Argentina; NZFS = New Zealand Forest Research Culture Collection, Rotorua, New Zealand.

morphs grouped in smaller lineages (labelled A to D, Fig. 1) outside or between the major genera.

For the compilation of the ITS data set, outgroups were selected for *Sporothrix* based on the LSU trees (Fig. 1). The lineages closest to *Sporothrix* were chosen and included species of *Fragosphaeria*, *Ceratocystiopsis* and Lineage C (Fig. 2). Attempts to include species from more genera such as *Ophiostoma* s. str. and from lineages A, B and D, resulted in data sets that were too variable to align appropriately, and such taxa were thus excluded from further analyses. The same group of taxa constituting the lineage defined as *Sporothrix* in the LSU trees (Fig. 1), again formed a well-supported lineage in the trees based on ITS data (Fig. 2). However, the ITS trees provided substantially more resolution than the LSU trees and revealed several lineages within the genus *Sporothrix*. Well-supported lineages (numbered 1 to 6) that corresponded with those in the *BT* (Fig. 3) and *CAL* (Fig. 4) trees, were recognized as species complexes. These complexes were defined following the criteria applied by De Beer & Wingfield (2013) in recognising the 18 species complexes they defined in the *Ophiostomatales*. Each complex was named based on the species that was first described in that complex (Fig. 2). The only exception was Lineage 3 that contained *S. schenckii* and the other human pathogens. Chen *et al.* (2016) argued against the use of the term “complex” in medical mycology for a clade such as this that includes well-defined species causing different disease symptoms, and that differ from each other in routes of transmission, virulence and antifungal susceptibility. In line with other recent publications dealing with *S. schenckii* and the other pathogenic species (Rodrigues *et al.* 2015a, 2015b, Zhang *et al.* 2015), we thus refer to Lineage 3 as the *Pathogenic Clade*. A few species did not form part of consistently supported lineages and were labelled as groups E to I to facilitate discussion.

Species of *Ceratocystiopsis* and Lineage C were used as outgroups in the *BT* data set because no *BT* sequences were available for *Fragosphaeria*. Apart from species complex 1, all four the other complexes defined based on ITS (Fig. 2), also had strong statistical support in the *BT* trees (Fig. 3). The *BT* sequences obtained mostly spanned exons 3, 4, 5, and the 5' part of exon 6, but the *BT* genes of different species had a variety of intron arrangements (Table 2 and Fig. 3). Most species lacked one to two of the introns, and the arrangements corresponded with the species complexes. Species complexes 1 and 2, and group E lacked both introns 3 and 4 and only contained intron 5 (-/4/5). Taxa in complexes 3, 4, 5 and 6, and groups F, G, H and I, all contained introns 3 and 5 but lacked intron 4 (3/4/5). The only exception was *O. nothofagi* that contained intron 4, but lacked intron 5 (?/4/-). The fragment of the latter species was too short to determine whether intron 3 was present or not. As more than 50% of basepairs from mostly introns were excluded from the analyses by Gblocks (see legend of Fig. 3), the trees obtained did not fully reflect differences in *BT* sequences between closely related taxa.

In the analyses of the *CAL* gene region (Fig. 4), only Lineage C was included as outgroup because *CAL* sequences were not available for *Fragosphaeria* and *Ceratocystiopsis*. The topology of the trees generally reflected those of the ITS and *BT* trees, and all six species complexes were statistically supported. The intron arrangements for the *CAL* gene region were less variable than those of *BT*, with only two patterns observed (Table 2 and Fig. 3). All taxa in *Sporothrix* for which *CAL* data were available had a pattern of 3/4/-, with the only exceptions found in *O. nothofagi* and *S. brunneoviolacea* (in Group I), which had all three introns (3/4/5). Similar to those for

*BT*, the *CAL* trees did not fully reflect sequence differences between closely related taxa because a considerable portion of the more informative intron data had been excluded from the analyses.

## TAXONOMY AND NOMENCLATOR

Based on phylogenetic analyses of four gene regions (Figs 1–4) we conclude that the previously recognised *S. schenckii*–*O. stenoceras* species complex in *Ophiostoma* s. lat., represents a distinct genus in the *Ophiostomatales*. This genus is *Sporothrix*, with *S. schenckii* as type species, and it is distinct from *Ophiostoma* s. str., defined by *O. piliferum* as type species. Based on one fungus one name principles, we redefine *Sporothrix*, which previously included only asexual morphs (de Hoog 1974), such that the generic diagnosis now also reflects the morphology of species with known sexual morphs.

***Sporothrix*** Hektoen & C.F. Perkins, J. Exp. Med. 5: 80. 1900. emend. Z.W. de Beer, T.A. Duong & M.J. Wingf.

*Synonyms:* *Sporotrichopsis* Gueguen. In De Beurmann & Gougerot, Archs Parasit. 15: 104. 1911. [type species *S. beurmannii*; nom. inval., Art. 38.1]

*Dolichoascus* Thibaut & Ansel. In Ansel & Thibaut, Compt. Rend. Hebd. Séances Acad. Sci. 270: 2173. 1970. [type species *D. schenckii*; nom. inval., Art. 40.1]

*Sporothrix* section *Sporothrix* Weijman & de Hoog, Antonie van Leeuwenhoek 51: 118. 1985.

*Ascocarps* dark brown to black, bases globose; necks straight or flexuous, cylindrical, tapering slightly to apex, up to 1 600 µm long, brown to black; ostiole often surrounded by divergent, ostiolar hyphae, sometimes absent. *Asci* 8-spored, evanescent, globose to broadly clavate. *Ascospores* hyaline, aseptate, lunate, allantoid, reniform, orange section-shaped, sheath absent. *Asexual states* micronematous, mycelial, hyaline or occasionally pigmented conidia produced holoblastically on denticulate conidiogenous cells. Phylogenetically classified in the *Ophiostomatales*.

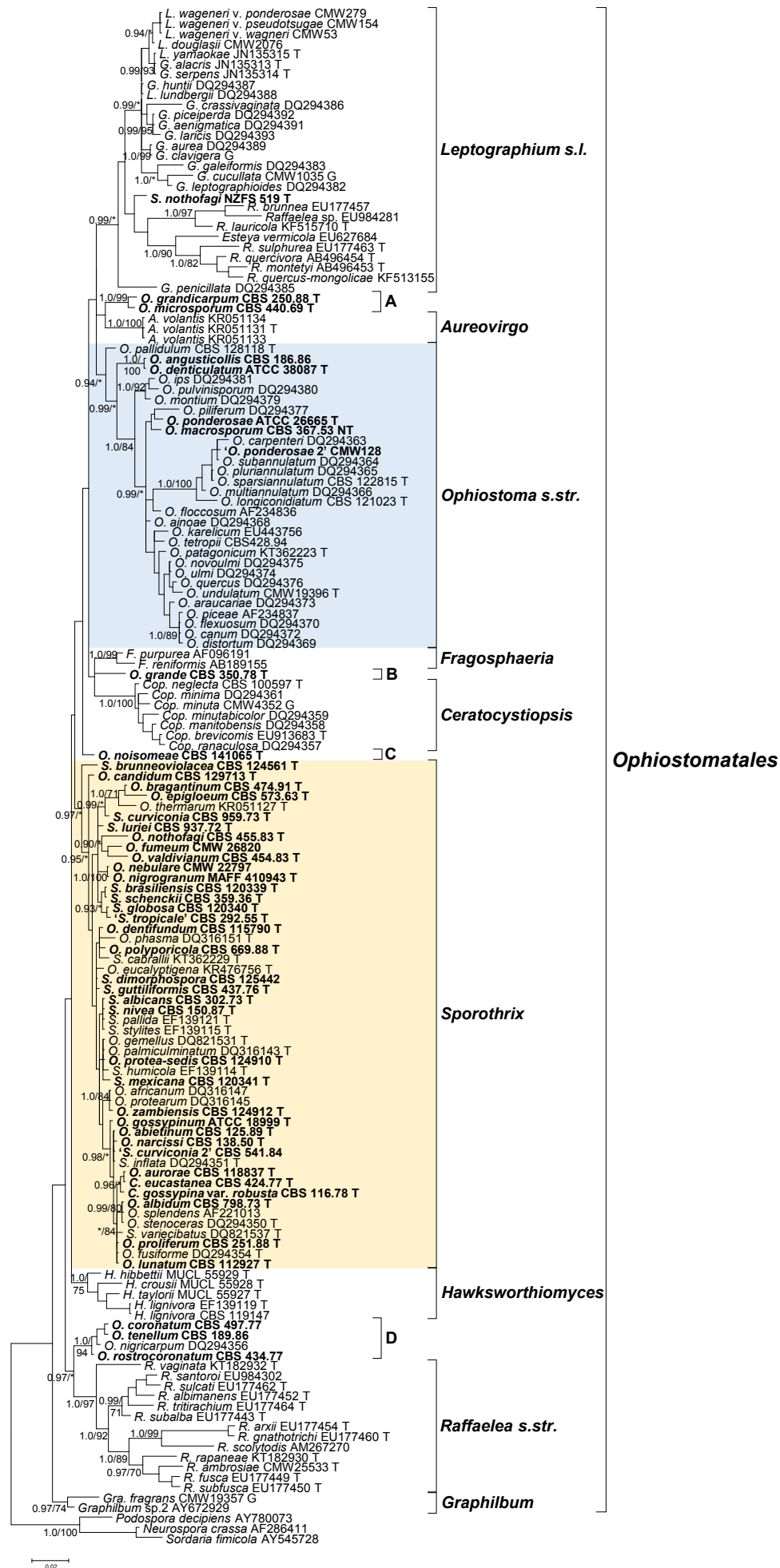
*Type species:* *Sporothrix schenckii* Hektoen & C.F. Perkins

*Note:* The synonymies of *Sporotrichopsis* and *Dolichoascus* with *Sporothrix* are discussed in the Notes accompanying *S. schenckii* below.

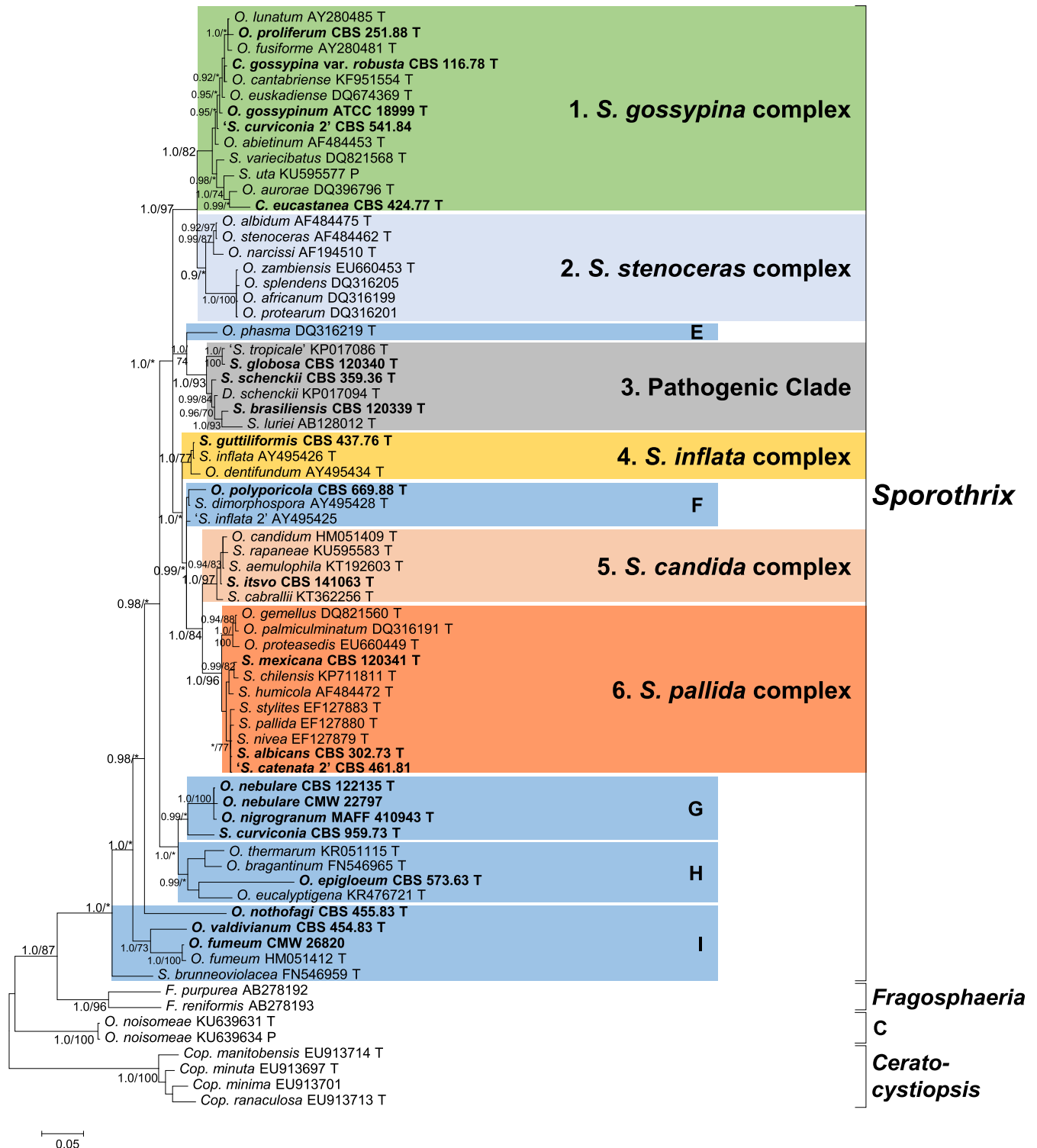
- Sporothrix abietina*** (Marm. & Butin) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817561. *Basionym:* *Ophiostoma abietinum* Marm. & Butin, Sydowia 42: 194. 1990.

*Notes:* De Beer *et al.* (2003) incorrectly treated several isolates of *S. abietina*, including the ex-type, as *O. nigrocarpum* (now *O. nigricarpum*). Aghayeva *et al.* (2004) showed that these two species are distinct, and that De Beer's isolates all grouped with the ex-type isolate of *S. abietina*, that also represented the species in our analyses and formed part of the *S. gossypina* complex (Figs 2–4). This species should not be confused with *Leptographium abietinum* (Peck) M.J. Wingf. that resides in the *Grosmannia penicillata* complex (De Beer & Wingfield 2013, De Beer *et al.* 2013).









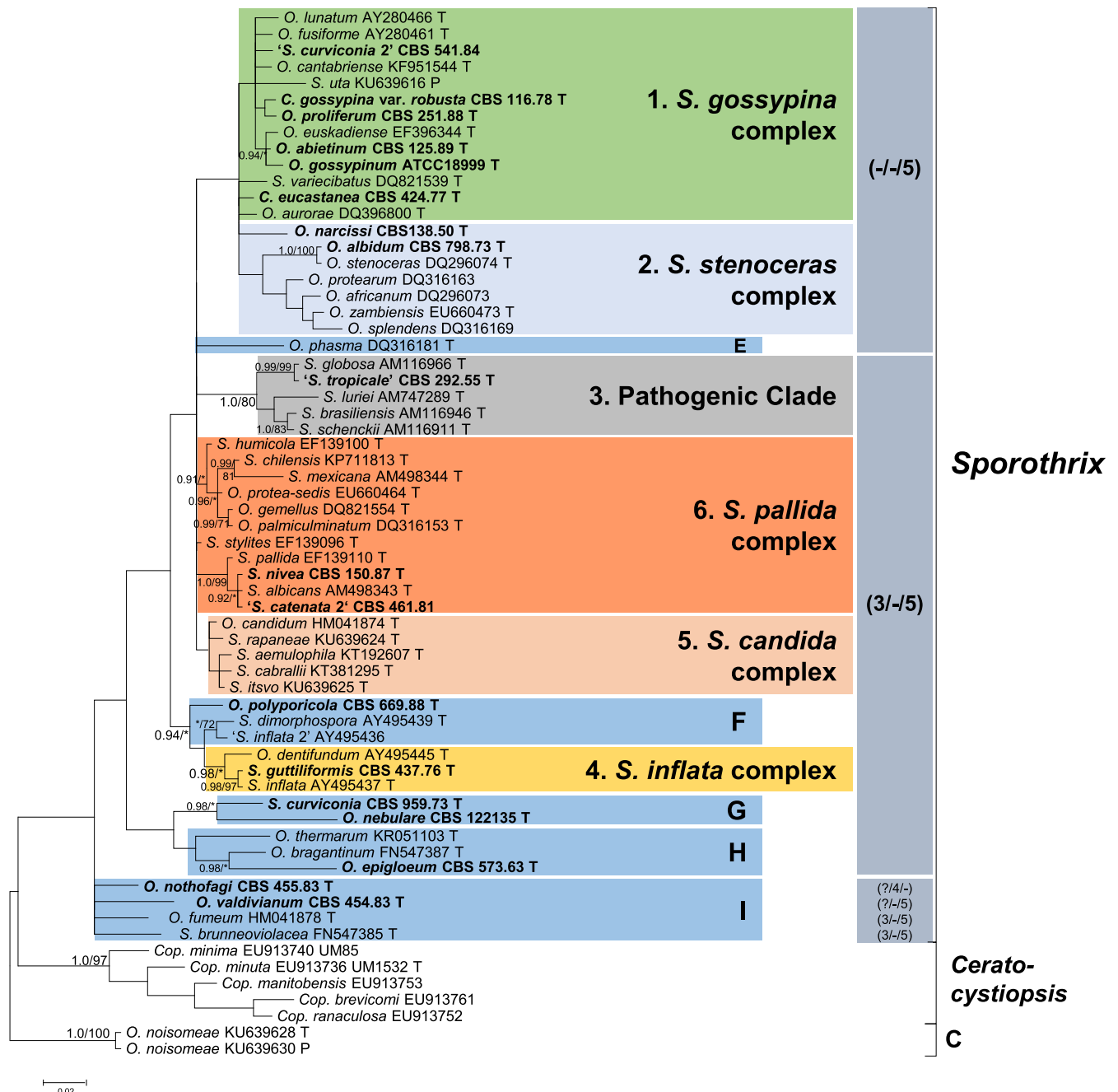
**Fig. 2.** Bayesian phylogram derived from analyses of the ITS dataset (70 taxa included, 516 characters remained after treatment with Gblocks, 259 of which were variable). The tree was constructed using MrBayes 3.2.5 using the GTR+G nucleotide substitution model. Bayesian posterior probabilities (BI) and maximum likelihood (ML) bootstrap supports are indicated at nodes as BI/ML. \* = no support or bootstrap support values <70% and posterior probabilities <0.90. Sequences for taxa in bold-type were generated in this study. T = ex-holotype; P = ex-paratype.

**2. *Sporothrix aemulophila*** T. Musvuugwa *et al.*, Antonie van Leeuwenhoek 108: 945. 2015.

**3. *Sporothrix africana*** G.J. Marais & M.J. Wingf., Mycol. Res. 105: 242. 2001. [as '*africanum*']  
Synonym: *Ophiostoma africanum* G.J. Marais & M.J. Wingf., Mycol. Res.105: 241. 2001.

Note: Forms part of the *S. candida* complex (Figs 2–4).

**Fig. 1.** Phylogram depicts the taxonomic relationship of *Sporothrix*, *Ophiostoma* s. str. and other genera in the *Ophiostomatales* based on LSU sequences. The tree was constructed using MrBayes 3.2.5 using the GTR+G nucleotide substitution model. The aligned dataset included 151 taxa (730 total characters), 696 characters remained after treatment with Gblocks, 237 of which were variable. Bayesian posterior probabilities (BI) and maximum likelihood (ML) bootstrap supports are indicated at nodes as BI/ML. \* = no support or bootstrap support values <70% and posterior probabilities <0.90. Sequences for taxa in bold-type were generated in this study. T = ex-holotype; NT = ex-neotype; P = ex-paratype.



**Fig. 3.** Bayesian phylogram derived from analyses of the BT dataset (64 taxa included, 245 characters remained after treatment with Gblocks, 85 of which were variable). Presence (intron numbers 3, 4 and 5) or absence (-) of introns are indicated in the column on the right. The tree was constructed using MrBayes 3.2.5 using the GTR+G nucleotide substitution model. Bayesian posterior probabilities (BI) and maximum likelihood (ML) bootstrap supports are indicated at nodes as BI/ML. \* = no support or bootstrap support values <70% and posterior probabilities <0.90. Sequences for taxa in bold-type were generated in this study. T = ex-holotype; P = ex-paratype.

Note: Forms part of the *S. stenoceras* complex (Figs 2 and 3).

**4. *Sporothrix aurorae*** (X.D. Zhou & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817562.

*Basionym:* *Ophiostoma aurorae* X.D. Zhou & M.J. Wingf., Stud. Mycol. 55: 275. 2006.

Note: Forms part of the *S. gossypina* complex (Figs 2–4).

**5. *Sporothrix bragantina*** (Pfenning & Oberw.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817564.

*Basionym:* *Ophiostoma bragantinum* Pfenning & Oberw., Mycotaxon 46: 381. 1993.

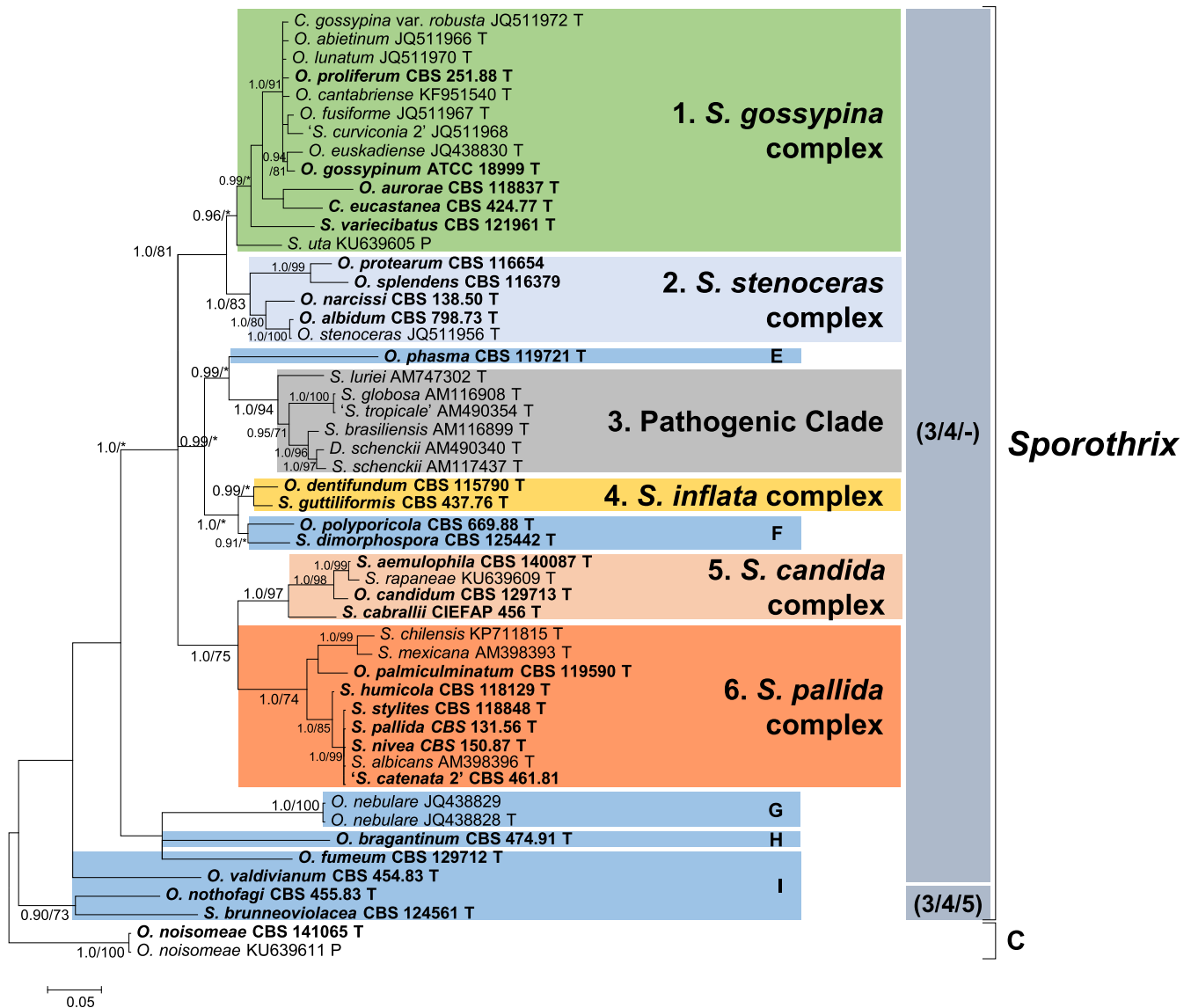
Note: Forms part of Lineage H (Figs 2–4).

**6. *Sporothrix brasiliensis*** Marimon *et al.*, J. Clin. Microbiol. 45: 3203. 2007.

Note: Forms part of the *Pathogenic Clade* (Figs 2–4).

**7. *Sporothrix brunneoviolacea*** Madrid *et al.*, Mycologia 102: 1199. 2010.

Notes: Madrid *et al.* (2010a) described some isolates previously referred to as *S. inflata* by Halmshlager & Kowalski (2003) and Aghayeva *et al.* (2005), as *S. brunneoviolacea*. In all four of our phylogenies, this species grouped peripheral to the core species complexes in *Sporothrix* (Figs 1–4), in an unsupported group



**Fig. 4.** Bayesian phylogram derived from analyses of the CAL dataset (51 taxa included, 530 characters after Gblock, of which 293 were variable character). Presence (intron numbers 3, 4 and 5) or absence (-) of introns are indicated in the column on the right. The tree was constructed using MrBayes 3.2.5 using the GTR+G nucleotide substitution model. Bayesian posterior probabilities (BI) and maximum likelihood (ML) bootstrap supports are indicated at nodes as BI/ML. \* = no support or bootstrap support values <70% and posterior probabilities <0.90. Sequences for taxa in bold-type were generated in this study. T = ex-holotype; P = ex-paratype.

(Group I, Figs 2–4). Although it differs from most *Sporothrix* spp. in its CAL intron arrangement (Table 2), it is retained in *Sporothrix* for the present.

**8. *Sporothrix cabralii*** de Errasti & Z.W. de Beer, Mycol. Prog. 15(17): 10. 2016.

Note: Forms part of the *S. candida* complex (Figs 2–4).

**9. *Sporothrix candida*** (Kamgan *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817565. *Basionym:* *Ophiostoma candidum* Kamgan *et al.*, Mycol. Progress 11: 526. 2012.

Note: The first taxon to be described in this newly defined complex and thus the name-bearing species of the *S. candida* complex (Figs 2–4).

**10. *Sporothrix cantabriensis*** (P. Romón *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817566.

*Basionym:* *Ophiostoma cantabriense* P. Romón *et al.*, Antonie van Leeuwenhoek 106: 1175. 2014.

Note: Forms part of the *S. gossypina* complex (Figs 2–4).

**11. *Sporothrix chilensis*** A.M. Rodrigues *et al.*, Fung. Biol. 120: 256. 2016.

Note: Forms part of the *S. pallida* complex (Figs 2–4).

**12. *Sporothrix curviconia*** de Hoog, Stud. Mycol. 7: 33. 1974.

Notes: The ex-type isolate (CBS 959.73) from *Terminalia* in the Ivory Coast forms part of group G (Figs 2 and 3) and its placement in *Sporothrix* is confirmed. Sequences of another isolate (CBS 541.84) previously treated as *S. curviconia* from *Pinus radiata* in Chile are labelled in our trees as '*S. curviconia* 2'. This isolate grouped close to *O. abietinum* and related species in the *S. gossypina* complex (Figs 2–4) and most likely represents a novel taxon.

**Table 2.** A comparative summary of morphological, ecological, and genetic characters of species of *Sporothrix*, as well *Ophiostoma* spp. with sporothrix-like asexual states of uncertain generic placement.

Group	Species	Sexual state	Conidia	Colony	Pathogen/ Soil	Host	Beetle/ mite	BT Introns	CAL Introns	Continent
<b>SPOROTHRIX</b>										
<b>Pathogenic Clade</b>	<i>S. brasiliensis</i>	n	h, p	br	p			3/-/5	3/4/-	South America
	<i>S. globosa</i>	n	h, p	br	p, s	hay		3/-/5	3/4/-	Asia, Europe, North America, South America
	<i>S. luriei</i>	n	h	w	p			3/-/5	3/4/-	Africa
	<i>S. schenckii</i>	n	h, p	br	p, s	h, hay		3/-/5	3/4/-	Africa, Asia, Australasia, Europe, Central-, North- & South America
<b>S. candida complex</b>	<i>S. aemulophila</i>	y	h	w		h	ab	?/-/5	3/4/-	Africa
	<i>S. cabralii</i>	n	h	w		h	ab	3/-/5	3/4/-	South America
	<i>S. candida</i>	y	h	w		h		3/-/5	3/4/-	Africa
	<i>S. itsvo</i>	y	h	w		h		?/-/5		Africa
	<i>S. rapaneae</i>	y	h	w		h		?/-/5	3/4/-	Africa
<b>S. gossypina complex</b>	<i>S. abietina</i>	y	h	w	s?	c	bb	?/-/5	3/4/-	Africa, Asia, Australasia, Europe, North America
	<i>S. aurorae</i>	y	h	h-w	s	c	bb	-/-/5	3/4/-	Africa
	<i>S. cantabriensis</i>	n	h	w	s?	c	bb	?/-/5	3/4/-	Europe
	<i>S. eucastanea</i>	y	h	w		h		?/-/5	3/4/-	North America
	<i>S. euskadiensis</i>	y	h	w	s?	c	bb	?/-/5	3/4/-	Europe
	<i>S. fusiformis</i>	y	h	w		h		?/-/5	3/4/-	Asia, Europe
	<i>S. gossypina</i>	y	h	w		c	bb	?/-/5	3/4/-	North America
	<i>S. lunata</i>	y	h	w		h		?/-/5	3/4/-	Europe
	<i>S. prolifera</i>	y	h	w		h		-/-/5	3/4/-	Europe
	<i>S. rossii</i>	y	h	w		c	bb	?/-/5	3/4/-	North America
	<i>S. uta</i>	y	h	w		h		?/-/5	3/4/-	Africa
	<i>S. variecibatus</i>	n	h	w		p	m	3/-/5	3/4/-	Africa
<b>S. inflata complex</b>	<i>S. dentifunda</i>	y	h	h-w		h		3/-/5	3/4/-	Europe
	<i>S. guttiformis</i>	n	h	w	s			3/-/5	3/4/-	Asia
	<i>S. inflata</i>	n	h, p	g	s			3/-/5	3/4/-	Europe
<b>S. pallida complex</b>	<i>S. chilensis</i>	n	h	w	p, s			3/-/5	3/4/-	South America
	<i>S. gemella</i>	y	h	w		p	m	3/-/5	3/4/-	Africa
	<i>S. humicola</i>	n	h	w	s			?/-/5	3/4/-	Africa
	<i>S. mexicana</i>	n	h, p	br	p, s	h		3/-/5	3/4/-	Europe, Central America, South America
	<i>S. pallida</i>	n	h	w	p, s	f		?/-/5	3/4/-	Asia, Europe
	<i>S. palmiculminata</i>	y	h	h-w		p	m	3/-/5	3/4/-	Africa
	<i>S. protea-sedis</i>	y	h	w		p	m?	3/-/5		Africa
	<i>S. stylites</i>	n	h	w	s	h, c		?/-/5	3/4/-	Africa
<b>S. stenoceras complex</b>	<i>S. africana</i>	y	h	w		p		?/-/5		Africa
	<i>S. narcissi</i>	y	h	w	s	bulbs		?/-/5	3/4/-	Australasia, Europe, North America
	<i>S. protearum</i>	y	h	w		p		?/-/5	3/4/-	Africa
	<i>S. splendens</i>	y	h	w		p	m	-/-/5	3/4/-	Africa
	<i>S. stenoceras</i>	y	h	h-w-br	p, s	h, c		?/-/5	3/4/-	Africa, Asia, Australasia, Europe, North America, South America
	<i>S. zambiensis</i>	y	h	w		p	m?	-/-/5		Africa
<b>Group E</b>	<i>S. phasma</i>	y	h	h-w		p	m	-/-/5	3/4/-	Africa
<b>Group F</b>	<i>S. dimorphospora</i>	n	h, p	w	s	h		3/-/5	3/4/-	Europe, North America, South America
<b>Group G</b>	<i>S. polyporicola</i>	y	h	br		f		3/-/5	3/4/-	Europe
	<i>S. curviconia</i>	n	h	w		h		3/-/5		Africa
	<i>S. nebularis</i>	y	h	w	s?	c	bb	3/-/5	3/4/-	Europe
<b>Group H</b>	<i>S. nigrograna</i>	y	h	w		c	bb			Asia
	<i>S. bragantina</i>	y	h, p	h	s			3/-/5	3/4/-	South America
	<i>S. epigloea</i>	y	h	h-w		f		3/-/5		South America
	<i>S. eucalyptigena</i>	y	h	w		h				Australasia
<b>Group I</b>	<i>S. thermara</i>	n	h	w		h	ab	3/-/5		Africa
	<i>S. brunneoviolacea</i>	n	h, p	w, g	s	h		3/-/5	3/4/5	Europe
	<i>S. dombeyi</i>	y	h	w, g		h		?/4/-	3/4/5	South America
	<i>S. fumea</i>	y	h	g		h	c	3/-/5	3/4/-	Africa
<b>OTHER GENERA</b>										
<b>Hawksworthiomyces</b>	<i>H. lignivora</i>	n	h	olivaceous		h		-/4/5		Africa
<b>Leptographium s.l.</b>	<i>S. nothofagi</i>	n	h	w, g		h	ab	3/4/-	3/4/5	Australasia
<b>Ophiostoma s.str.</b>	<i>O. angusticollis</i>	y	h	h-w		c		3/4/5		North America
	<i>O. denticulatum</i>	y	h	w-br		c	ab	3/4/5	3/4/-	North America
	<i>O. macrosporum</i>	y	h	br		c	bb	3/4/-		Europe
	<i>O. ponderosae</i>	y	h	w-br		c				USA
	<i>O. sejunctum</i>	y	h	h-w		c	bb			Europe
<b>Lineage A</b>	<i>O. grandicarpum</i>	y	h	w		h		3/-/5		Europe
	<i>O. microsporum</i>	y	h	w		h		3/-/5		USA
<b>Lineage B</b>	<i>O. ambrosium</i>	y	h	h-g		h	ab			Europe
	<i>O. grande</i>	y	h	w		f			3/4/5	South America
<b>Lineage C</b>	<i>O. noisomeae</i>	y	h, p	w-b		h		3/4/5		Africa
<b>Lineage D</b>	<i>O. coronatum</i>	y	h	w		c		3/-/5	3/4/5	North America
	<i>O. nigricarpum</i>	y	h	h		c	bb	3/-/5		North America
	<i>O. rostrocoronatum</i>	y	h	w		h		3/-/5	3/4/5	North America
	<i>O. tenellum</i>	y	h	w-b		c	bb	3/-/5	3/4/5	North America

**Sexual state** y = yes, n = no; **Conidia** h = hyaline, p = pigmented blastoconidia; **Colony** w = white, h = hyaline, g = grey, b = black, br = brown; **Pathogen/Soil** p = human/mammal pathogen, s = from soil; **Host** c = conifer; p = *Protea* infructescence, h = hardwood, f = macrofungus fruiting body; **Beetle/mite** bb = bark beetle, ab = ambrosia beetle, c = cerambycid, m = mite



13. *Sporothrix dentifunda* (Aghayeva & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817567.  
*Basionym:* *Ophiostoma dentifundum* Aghayeva & M.J. Wingf., Mycol. Res. 109: 1134. 2005.

Note: Forms part of the *S. inflata* complex (Figs 2–4).

14. *Sporothrix dimorphospora* (Roxon & S.C. Jong) Madrid *et al.*, Mycologia 102: 1199. 2010.  
*Basionym:* *Humicola dimorphospora* Roxon & S.C. Jong, Canad. J. Bot. 52: 517. 1974.

Note: Forms part of Clade F (Figs 2–4).

15. *Sporothrix dombeyi* Z.W. de Beer, T.A. Duong & M.J. Wingf., **nom. nov.** MycoBank MB817568.  
*Synonyms:* *Ceratocystis nothofagi* Butin. In Butin & Aquilar, Phytopathol. Z. 109: 84. 1984.  
*Ophiostoma nothofagi* (Butin) Rulamort, Bull. Soc. Bot. Centre-Ouest, n.s. 17: 192. 1986.

Notes: Based on cultural morphology and in the absence of DNA sequence data, De Beer *et al.* (2013) suggested that *O. nothofagi* might be related to species such as *O. piliferum* or *O. pluriannulatum* rather than to the *S. schenckii*-*O. stenoceras* complex. However, our sequences of the ex-type isolate confirms its placement in *Sporothrix* (Group I, Figs 1–4). It thus needed to be transferred to *Sporothrix*. However, since the epithet *nothofagi* is unavailable in *Sporothrix* because of *Sporothrix nothofagi* Gadgil & M.A. Dick [Art. 6.11], we provided a new name based on the epithet of its original host tree (*Nothofagus dombeyi*), rather than the genus of the host. *Sporothrix nothofagi* Gadgil & M.A. Dick is not closely related to the latter species and is placed in *Leptographium s. lat.* (see below under species of uncertain generic status in the *Ophiostomatales*).

16. *Sporothrix epigloea* (Guerrero) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817569.  
*Basionym:* *Ceratocystis epigloea* Guerrero, Mycologia 63: 921. 1971. [as 'epigloeum']  
*Synonym:* *Ophiostoma epigloeum* (Guerrero) de Hoog, Stud. Mycol. 7: 45. 1974.

Note: Forms part of group H in *Sporothrix* (Figs 2 and 3).

17. *Sporothrix eucalyptigena* (Barber & Crous) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817570.  
*Basionym:* *Ophiostoma eucalyptigena* Barber & Crous, Persoonia 34: 193. 2015.

Note: Forms part of group H in *Sporothrix* (Fig. 2).

18. *Sporothrix eucastaneae* (R.W. Davidson) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817571.  
*Basionym:* *Ceratocystis eucastaneae* R.W. Davidson, Mycologia 70: 856. 1978.

Notes: *Ceratocystis eucastanea* was treated by Upadhyay (1981), Seifert *et al.* (1993) and De Beer *et al.* (2013) as

synonym of *O. stenoceras*. However, our sequences of the ex-type isolate (Figs 2–4) confirmed that this is a distinct species grouping close to *O. aurorae* in the *S. gossypina* complex.

19. *Sporothrix euskadiensis* (P. Romón *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817572.  
*Basionym:* *Ophiostoma euskadiense* P. Romón *et al.*, Mycologia 106: 125. 2014.

Note: Forms part of the *S. gossypina* complex (Figs 2–4).

20. *Sporothrix fumea* (Kamgan *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817573.  
*Basionym:* *Ophiostoma fumeum* Kamgan *et al.*, Mycol. Progress 11: 527. 2012.

Note: Forms part of Group I (Figs 2–4).

21. *Sporothrix fusiformis* (Aghayeva & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817574.  
*Basionym:* *Ophiostoma fusiforme* Aghayeva & M.J. Wingf., Mycologia 96: 875. 2004.

Note: Forms part of the *S. gossypina* complex (Figs 2–4).

22. *Sporothrix gemella* (Roets *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817575.  
*Basionym:* *Ophiostoma gemellus* Roets, Z.W. de Beer & Crous, Mycologia 100: 504. 2008.

Note: Forms part of a *Protea*-associated subclade in the *S. pallida* complex (Figs 2 and 3).

23. *Sporothrix globosa* Marimon *et al.*, J. Clin. Microbiol. 45: 3203. 2007.  
*Synonym:* *Sporotrichum tropicale* D. Panja *et al.*, Indian Med. Gaz. 82: 202. 1947. [*nom. inval.*, Art. 36.1]

Notes: *Sporothrix globosa* groups in the *Pathogenic Clade*. *Sporotrichum tropicale* was listed as synonym of *S. schenckii* by de Hoog (1974). The *BT* sequence for the original isolate of the latter species is identical to the *S. globosa* ex-type isolate (Fig. 3), while the *LSU*, *ITS* and *CAL* sequences of the two isolates respectively differ in 1, 2, and 1 positions (Figs 1, 2 and 4). These two species should be considered synonyms as suggested by de Hoog (1974). Since the older name *S. tropicale* was invalidly published without a Latin diagnosis, the name *S. globosa* takes preference.

24. *Sporothrix gossypina* (R.W. Davidson) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817576.  
*Basionym:* *Ceratocystis gossypina* R.W. Davidson, Mycologia 63: 12. 1971.  
*Synonym:* *Ophiostoma gossypinum* (R.W. Davidson) J. Taylor, Mycopath. Mycol. Appl. 38: 112. 1976.

Notes: Davidson (1971) distinguished between *O. gossypinum* and *C. gossypina* var. *robusta* (= *S. rossii*, see below) based on peritheciomorphology. Upadhyay (1981) treated both species as synonyms of *O. stenoceras*. Hausner & Reid (2003) showed

that the LSU sequence of the ex-type isolate (ATCC 18999) of *O. gossypinum* differs from that of *O. stenoceras*. Our results confirmed that the three species are distinct, and that *S. gossypina* groups close to, but distinct from *O. abietinum* and related species in species complex 1 (Figs 1–4). As the first species to be described it becomes the name-bearing species of this complex.

**25. *Sporothrix guttuliformis*** de Hoog, Persoonia 10: 62. 1978.

Notes: Sequences produced in the present study for the ex-type isolate of this species place it in *S. inflata* complex (Figs 2–4). However, earlier studies using the same isolate showed that this species was different from *S. schenckii* in physiology (de Hoog et al. 1985, de Hoog 1993) and septal pore structure (Smith & Batenburg-Van der Vegte 1985). The ex-type isolate must thus be reconsidered carefully to determine whether it still corresponds with the original description.

**26. *Sporothrix humicola*** de Mey. et al., Mycologia 100: 656. 2008.

Note: Groups in the *S. pallida* complex (Figs 2–4).

**27. *Sporothrix inflata*** de Hoog, Stud. Mycol. 7: 34. 1974.

Notes: Aghayeva et al. (2005) showed that isolates previously treated as *S. inflata* separated in four clades, one of which represented *S. inflata* s. str. This is the name-bearing species of the *S. inflata* complex in our analyses (Figs 2 and 3). The second group was subsequently described as representing a new species, *S. brunneoviolacea*, while the third group included the ex-type isolate of *Humicola dimorphospora*, which was transferred to *Sporothrix* by Madrid et al. (2010a) (see *S. dimorphospora* above). The fourth group, designated in our trees as ‘*S. inflata* 2’ in clade F (Figs 2 and 3), remains to be described as a new taxon.

**28. *Sporothrix itsvo*** Musvuugwa et al., Antonie van Leeuwenhoek 109: 885. 2016.

Note: Forms part of the *S. candida* complex (Figs 2 and 3).

**29. *Sporothrix lunata*** (Aghayeva & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817577.  
Basionym: *Ophiostoma lunatum* Aghayeva & M.J. Wingf., Mycologia 96: 874. 2004.

Note: Forms part of the *S. gossypina* complex (Figs 2–4).

**30. *Sporothrix luriei*** (Ajello & Kaplan) Marimon et al., Med. Mycol. 46: 624. 2008.  
Basionym: *S. schenckii* var. *luriei* Ajello & Kaplan, Mykosen 12: 642. 1969.

Note: Forms part of the *Pathogenic Clade* (Figs 2–4).

**31. *Sporothrix mexicana*** Marimon et al., J. Clin. Microbiol. 45: 3203. 2007.

Note: Forms part of the *S. pallida* complex (Figs 2–4).

**32. *Sporothrix narcissi*** (Limber) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817578.  
Basionym: *Ophiostoma narcissi* Limber, Phytopathology 40: 493. 1950.  
Synonym: *Ceratocystis narcissi* (Limber) J. Hunt, Lloydia 19: 50. 1956.

Note: Forms part of the *S. stenoceras* complex.

**33. *Sporothrix nebularis*** (P. Romón et al.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817579.  
Basionym: *Ophiostoma nebulare* P. Romón et al., Mycologia 106: 125. 2014.

Note: Groups close to *S. nigrograna* in Group G (Figs 2–4).

**34. *Sporothrix nigrograna*** (Masuya) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817580.  
Basionym: *Ophiostoma nigrogranum* Masuya, Mycoscience 45: 278. 2004.

Notes: This species was listed by Masuya et al. (2013) as part of the *S. schenckii*–*O. stenoceras* complex. De Beer et al. (2013) suggested an affiliation with *Leptographium* s. lat. rather than with *Sporothrix* s. str. based on the hyalorhinocladia-like asexual morph and sheathed ascospores. However, our sequences of the ex-type isolate confirms its placement close to *S. nebularis* in Group G of *Sporothrix* (Figs 1 and 2).

**35. *Sporothrix pallida*** (Tubaki) Matsush., Icon. microfung. Matsush. lect. (Kobe): 143. 1975.  
Basionym: *Calcarisporium pallidum* Tubaki, Nagaoa 5: 13. 1955.  
Synonyms: *Sporothrix albicans* S.B. Saksena, Curr. Sci. 34: 318. 1965.  
*Sporothrix nivea* Kreisel & F. Schauer, J. Basic Microbiol. 25: 654. 1985.

Notes: *Sporothrix albicans* and *Calcarisporium pallidum* were treated by de Hoog (1974) as synonyms of *S. schenckii*. However, De Meyer et al. (2008) showed that these two species grouped with *S. nivea*, distinct from *S. schenckii*. *Sporothrix albicans* and *S. nivea* were thus synonymised with *S. pallida*, the oldest of the three names. Our data confirmed the synonymy of these species (Figs 2–4). Rodrigues et al. (2016) defined the lineage containing these and several other species as the *S. pallida* complex, a definition supported by our analyses.

**36. *Sporothrix palmiculminata*** (Roets et al.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817581.  
Basionym: *Ophiostoma palmiculminatum* Roets et al., Stud. Mycol. 55: 208. 2006.

Note: Groups in the *S. pallida* complex (Figs 2–4).

**37. *Sporothrix phasma*** (Roets et al.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817582.

*Basionym:* *Ophiostoma phasma* Roets, Z.W. de Beer & M.J. Wingf., *Stud. Mycol.* 55: 207. 2006.

*Note:* Forms a unique lineage between the other species complexes and groups in *Sporothrix* (Lineage E, [Figs 2–4](#)).

- 38. *Sporothrix polyporicola*** (Constant. & Ryman) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817583.

*Basionym:* *Ophiostoma polyporicola* Constant. & Ryman, *Mycotaxon* 34: 637. 1989.

*Note:* Groups close to *S. dimorphospora* in Lineage F ([Figs 2–4](#)).

- 39. *Sporothrix prolifera*** (Kowalski & Butin) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817584.

*Basionym:* *Ceratocystis prolifera* Kowalski & Butin, *J. Phytopathol.* 124: 245. 1989.

*Synonym:* *Ophiostoma proliferum* (Kowalski & Butin) Rulamort, *Bull. Soc. Bot. Centre-Ouest, n.s.* 21: 511. 1990.

*Note:* Groups in the *S. gossypinum* complex ([Figs 2–4](#)).

- 40. *Sporothrix protearum*** G.J. Marais & M.J. Wingf., *Canad. J. Bot.* 75: 364. 1997.

*Synonym:* *Ophiostoma protearum* G.J. Marais & M.J. Wingf., *Canad. J. Bot.* 75: 363. 1997.

*Note:* Groups in a subclade including only species from *Protea* in the *S. stenoceras* complex ([Figs 2–4](#)).

- 41. *Sporothrix protea-sedis*** (Roets *et al.*) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817585.

*Basionym:* *Ophiostoma protea-sedis* Roets *et al.*, *Persoonia* 24: 24. 2010.

*Note:* Groups in the *S. pallida* complex ([Figs 2 and 3](#)).

- 42. *Sporothrix rapanaeae*** Musvuugwa *et al.*, *Antonie van Leeuwenhoek* 109: 885. 2016.

*Note:* Groups in the *S. candida* complex ([Figs 2 and 3](#)).

- 43. *Sporothrix rossii*** Z.W. de Beer, T.A. Duong & M.J. Wingf., **nom. nov.** MycoBank MB817586.

*Synonym:* *Ceratocystis gossypina* var. *robusta* R.W. Davidson, *Mycologia* 63: 13. 1971.

*Notes:* Davidson (1971) distinguished between *Ceratocystis gossypina* (now *Sporothrix gossypina*) and *C. gossypina* var. *robusta* based on perithecial morphology. Subsequent authors treated both species as synonyms of *O. stenoceras* (Upadhyay 1981, Seifert *et al.* 1993). Hausner & Reid (2003) showed that *O. gossypinum* is distinct from *O. stenoceras* based on LSU data. Villarreal *et al.* (2005) produced an ITS sequence of the ex-type isolate of *C. gossypina* var. *robusta*, and because that sequence (AY924388) was identical to that of the ex-type of *O. stenoceras*, De Beer & Wingfield (2013) treated *C. gossypina* var. *robusta* as a synonym of *O. stenoceras*. However, LSU, ITS, BT and CAL sequences produced for the ex-holotype isolate in the present study clearly separated the two taxa ([Figs 1–4](#)), necessitating a new combination for this name. To avoid

confusion with *Sporothrix gossypina* and with *Grosmannia robusta* (R.C. Rob. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf. [= *Ophiostoma robustum* (R.C. Rob. & R.W. Davidson) T.C. Harr.], we have designated a new epithet, based on the first name of the original author of this species, Ross W. Davidson. The description for *S. rossii* is the same as the original description of *C. gossypina* var. *robusta* (Davidson 1971), which is based on the holotype (RWD 609-D = BPI 595661) and ex-holotype isolate (CBS 116.78 = CMW 1118) from which sequences were obtained in the present study. *Sporothrix rossii* groups in the *S. gossypina* complex ([Figs 2–4](#)).

- 44. *Sporothrix schenckii*** Hektoen & C.F. Perkins, *J. Exp. Med.* 5: 77. 1900.

*Synonyms:* *Sporotrichum beurmannii* Matr. & Ramond, *Compt. Rend. Hebd. Séances Mém. Soc. Biol.* 2: 380. 1905.

*Sporotrichopsis beurmannii* (Matr. & Ramond) Gueguen. In De Beurmann & Gougerot, *Archs Parasit.* 15: 104. 1911. [*nom. inval.*, Art. 38.1]

*Sporothrix beurmannii* (Matr. & Ramond) Meyer & Aird, *J. Infect. Dis.* 16: 399. 1915.

*Dolichoascus schenckii* Thibaut & Ansel. In Ansel & Thibaut, *Compt. Rend. Hebd. Séances Acad. Sci.* 270: 2173. 1970. [*nom. inval.*, Art. 40.1]

*Note 1:* de Hoog (1974) listed several synonyms for *S. schenckii* from the medical literature predating 1940. The majority of those names are not listed here because material for these species is not available. Two exceptions are *S. beurmannii* and *D. schenckii* for reasons set out below.

*Note 2:* *Sporotrichopsis*, with *S. beurmannii* as type species, was published invalidly [Art. 38.1] as a provisional name by De Beurmann & Gougerot (1911) and was never validated. Davis (1920) argued convincingly that *S. beurmannii* should be treated as a synonym of *S. schenckii*. de Hoog (1974) followed this suggestion. The implication of the species synonymy is that *Sporotrichopsis*, if valid, would have been treated as a synonym of *Sporothrix*.

*Note 3:* *Dolichoascus schenckii*, the type species for *Dolichoascus*, was not validly published (Ansel & Thibaut 1970) because a holotype was not indicated [Art. 40.1] also resulting in an invalid genus name. Ansel & Thibaut (1970) and Thibaut (1972) suggested that *Dolichoascus* (*Endomycetaceae*) represented the sexual morph of *S. schenckii* due to the presence of what they described as endogenous ascospores. However, Mariat & Diez (1971) studied the isolate (CBS 938.72) of Ansel & Thibaut (1970) and suggested that the “ascospores” were in fact endoconidia. de Hoog (1974) argued that the name *Dolichoascus* could thus not be used for an anamorph genus based on the prevailing dual nomenclature principles dictated by Article 59 of the Seattle Code (Staffeu 1972). At present, the emended Article 59 of the Melbourne Code (McNeill *et al.* 2012) permits the use of the name *Dolichoascus* whether a sexual state is present or not. Because the ex-type isolate is still viable, lectotypification [Art. 9.2] and validation of the species and genus would be possible. However, Marimon *et al.* (2007) and Zhang *et al.* (2015) respectively produced a CAL and an ITS sequence for the *D. schenckii* isolate, confirming that it is conspecific with the ex-type of *S. schenckii* ([Figs 2 and 4](#)). There is consequently no need for lectotypification or validation



of the species or genus, as *Dolichoascus* becomes a valid synonym for *Sporothrix*.

**Note 4:** *Sporothrix schenckii* was treated for some years as asexual morph of *O. stenoceras* (Taylor 1970, Mariat 1971, de Hoog 1974). However, De Beer et al. (2003) showed that the two species were distinct based on ITS sequences, and this was confirmed in the present study with LSU, ITS, *BT* and *CAL* sequences (Figs 1–4). No sexual morph is currently known for *S. schenckii*.

- 45. *Sporothrix splendens*** G.J. Marais & M.J. Wingf., Mycol. Res. 98: 373. 1994.  
*Synonym:* *Ophiostoma splendens* G.J. Marais & M.J. Wingf., Mycol. Res. 98: 371. 1994.

**Note:** Forms part of the *S. stenoceras* complex (Figs 2–4).

- 46. *Sporothrix stenoceras*** (Robak) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817587.  
*Basionym:* *Ceratostomella stenoceras* Robak, Nyt Mag. Naturvid. Oslo 71: 214. 1932.  
*Synonyms:* *Ophiostoma stenoceras* (Robak) Nannf. In Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934.  
*Ceratocystis stenoceras* (Robak) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.  
*Ophiostoma albidum* Math.-Käärik, Medd. Skogsforskningsinst. 43: 52. 1953.  
*Ceratocystis albida* (Math.-Käärik) J. Hunt, Lloydia 19: 48. 1956.

**Note 1:** The asexual morph of *O. stenoceras* has often been referred to as *S. schenckii*, but De Beer et al. (2003) showed that the two species are distinct. Our analyses of all four gene regions supported the separation of the two species (Figs 1–4).

**Note 2:** *Ophiostoma albidum* was treated as synonym of *O. stenoceras* by de Hoog (1974), Upadhyay (1981) and Seifert et al. (1993). Hausner & Reid (2003) and De Beer et al. (2003) respectively showed that LSU and ITS sequences of *O. albidum* are identical to those of *O. stenoceras* (Figs 1 and 2). *BT* and *CAL* data produced in the present study for the ex-type isolates of both these species (Figs 3 and 4), confirmed that *O. albidum* is a synonym of *S. stenoceras*.

- 47. *Sporothrix stylites*** de Mey. et al., Mycologia 100: 656. 2008.

**Note:** Forms part of the *S. pallida* complex (Figs 2–4).

- 48. *Sporothrix thermara*** (J.A. van der Linde et al.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB817619.  
*Basionym:* *Ophiostoma thermarum* J.A. van der Linde et al., Antonie van Leeuwenhoek 109: 595. 2016.

**Note:** Forms part of Group H (Figs 2 and 3).

- 49. *Sporothrix uta*** Musvuugwa et al., Antonie van Leeuwenhoek 109: 887. 2016.

**Note:** Forms part of the *S. gossypina* complex (Figs 2–4).

- 50. *Sporothrix variecibatus*** Roets et al., Mycologia 100: 506. 2008.

**Note:** Forms part the *S. gossypina* complex (Figs 2–4).

- 51. *Sporothrix zambiensis*** (Roets et al.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MB817588.  
*Basionym:* *Ophiostoma zambiense* Roets et al., Persoonia 24: 24. 2010. [as 'zambiensis']

**Note:** Forms part the *S. stenoceras* complex (Figs 2 and 3).

## SPOROTHRIX SPP. AND SPECIES WITH SPOROTHRIX-LIKE ASEQUAL MORPHS CURRENTLY CLASSIFIED IN OTHER GENERA OF THE OPHIOSTOMATALES

This list includes species of *Ophiostomatales* where the sporothrix-like asexual morphs were provided with binomials in *Sporothrix* under the dual nomenclature system, or where our analyses confirmed the generic placement outside *Sporothrix* for the first time. Additional species with sporothrix-like asexual morphs but without a binomial in *Sporothrix*, and previously classified in other genera in the *Ophiostomatales* based on DNA sequence data, are listed by De Beer et al. (2013).

- 1. *Ophiostoma angusticollis*** (E.F. Wright & H.D. Griffin) M. Villarreal, Mycotaxon 92: 262. 2005.  
*Basionym:* *Ceratocystis angusticollis* E.F. Wright & H.D. Griffin, Canad. J. Bot. 46: 697. 1968.

**Notes:** Our LSU analyses suggest that *O. angusticollis* groups with *O. denticulatum* in a distinct lineage (Fig. 1) in *Ophiostoma* s. str. This supports the placement of the species by Villarreal et al. (2005) and De Beer & Wingfield (2013), who also showed that it groups with *O. sejunctum* based on ITS sequences. However, the isolate does not represent the holotype and typification needs to be resolved before a final conclusion can be made regarding the generic placement of this species.

- 2. *Ophiostoma denticulatum*** (R.W. Davidson) Z.W. de Beer & M.J. Wingf. In Seifert et al., The Ophiostomatoid Fungi: 252. 2013.  
*Basionym:* *Ceratocystis denticulata* R.W. Davidson, Mycologia 71: 1088. 1979.

**Notes:** De Beer et al. (2013) suggested that *O. denticulatum* might belong in the *S. schenckii*–*O. stenoceras* complex based on morphology. However, the species grouped with *O. angusticollis* distinct from *Sporothrix* in *Ophiostoma* s. str. in our LSU analyses (Fig. 1). In addition, its *BT* gene contains intron 4 (Table 2), which is absent in all species of *Sporothrix*.

- 3. *Ophiostoma macrosporum*** (Francke-Grosz.) Z.W. de Beer & M.J. Wingf. In Seifert et al., The Ophiostomatoid Fungi: 256. 2013.  
*Basionym:* *Trichosporum tingens* var. *macrosporum* Francke-Grosz., Medd. Skogsforskningsinst. 41: 27. 1952 [as '*Trichosporium tingens* var. *macrosporum*']  
*Synonyms:* *Ambrosiella macrospora* (Francke-Grosz.) L.R. Batra, Mycologia 59: 980. 1967.



*Hyalorhinocladiella macrospora* (Francke-Groszm.) TC. Harr. In Harrington *et al.*, Mycotaxon 111: 355. 2010.

Note: Forms a distinct lineage outside *Sporothrix* and close to *O. piliferum* in *Ophiostoma* s. str. (Fig. 1).

4. ***Ophiostoma ponderosae*** (T.E. Hinds & R.W. Davidson) Hausner *et al.*, Canad. J. Bot. 71: 1264. 1993.  
Basionym: *Ceratocystis ponderosae* T.E. Hinds & R.W. Davidson, Mycologia 67: 715. 1975.

Notes: According to De Beer *et al.* (2003) the ex-type of *O. ponderosae* (ATCC 26665 = RWD 900 = C87) had an ITS sequence identical to *O. stenoceras*. The original isolate died in our collection and we re-ordered the ex-type from ATCC (ATCC 26665 = RWD 900 = CMW 37953). The LSU sequence of the fresh isolate placed it close to *O. piliferum* in *Ophiostoma* s. str. (Fig. 1). Consequently, we do not accept the synonymy of *O. ponderosae* with *O. stenoceras*, exclude it from *Sporothrix* and consider it a distinct species of *Ophiostoma* s. str. The LSU and ITS sequences of another *O. ponderosae* isolate (CBS 496.77 = RWD 899) from the study of Hinds & Davidson (1975), grouped in the *O. pluriannulatum* complex (Fig. 1). It appears to represent an undescribed taxon in that complex, but for the interim it is labelled as '*O. ponderosae* 2'.

5. ***Sporothrix lignivora*** de Mey. *et al.*, Mycologia 100: 657. 2008.

Notes: This species groups in a distinct lineage of the *Ophiostomatales*, previously referred to as the *Sporothrix lignivora* complex, but recently defined as a new genus, *Hawksworthiomyces* (Fig. 1) (De Beer *et al.* 2016). The current name species name is *Hawksworthiomyces lignivora* (de Mey. *et al.*) Z.W. de Beer *et al.* (De Beer *et al.* 2016).

6. ***Sporothrix pirina*** (Goid.) Morelet, Ann. Soc. Sci. Nat. Arch. Toulon et du Var 44: 110. 1992. [as '*pirinum*']  
Basionym: *Hyalodendron pirinum* Goid., Boll. R. Staz. Patalog. Veget. Roma, N.S. 15: 136. 1935.

Note: This species was described as the anamorph of ***Ophiostoma catonianum*** (Goid.) Goid. and is currently treated as synonym of the latter species in the *O. ulmi* complex in *Ophiostoma* s. str. (Grobelaar *et al.* 2009, De Beer *et al.* 2013).

7. ***Sporothrix roboris*** (Georgescu & Teodoru) Grobelaar *et al.*, Mycol. Progress 8: 233. 2009.  
Basionym: *Hyalodendron roboris* Georgescu & Teodoru, Anal. Inst. Cerc. Exp. For. Rom., Ser 1. 11: 209. 1948.

Notes: *Sporothrix roboris* was described as the asexual morph of *Ophiostoma roboris* Georgescu & Teodoru (Grobelaar *et al.* 2009). Both *O. roboris* and *S. roboris* are now treated as synonyms of ***Ophiostoma quercus*** (Georgev.) Nannf. in the *O. ulmi* complex of *Ophiostoma* s. str. (De Beer & Wingfield 2013, De Beer *et al.* 2013).

8. ***Sporothrix subannulata*** Livingston & R.W. Davidson, Mycologia 79: 145. 1987.

Note: Initially described as asexual morph for ***Ophiostoma subannulatum*** Livingston & R.W. Davidson, but currently treated as its formal synonym in *Ophiostoma* s. str. (De Beer *et al.* 2013, De Beer & Wingfield 2013).

## SPOROTHRIX SPP. AND SPECIES WITH SPOROTHRIX-LIKE ASEQUAL MORPHS, BUT OF UNCERTAIN GENERIC STATUS IN THE OPHIOSTOMATALES

This list includes species for which sequence data place them in the *Ophiostomatales*, but not in one of the currently accepted genera. Taxa with sporothrix-like asexual morphs that resemble *Ophiostomatales*, but for which no sequence data are available are also included.

1. ***Ophiostoma ambrosium*** (Bakshi) Hausner, J. Reid & Klassen, Canad. J. Bot. 71: 1264. 1993.  
Basionym: *Ceratocystis ambrosia* Bakshi, Trans. Br. Mycol. Soc. 33: 116. 1950.

Notes: Griffin (1968), Upadhyay (1981), Hutchison & Reid (1988) and Seifert *et al.* (1993) treated *O. ambrosium* as synonym of *O. piliferum*, while Hunt (1956) and de Hoog (1974) treated it as a distinct species. In the phylogeny of De Beer & Wingfield (2013), a very short LSU sequence of *O. ambrosium* from Hausner *et al.* (1993b) grouped with *O. grande* in a lineage. We did not include the *O. ambrosium* sequence in our analyses because it was inordinately short, but *O. grande* grouped distinct from *Sporothrix* and all other genera in our analyses (Lineage B, Fig. 1).

2. ***Ophiostoma coronatum*** (Olchow. & J. Reid) M. Villarreal, Mycotaxon 92: 263. 2005.  
Basionym: *Ceratocystis coronata* Olchow. & J. Reid, Canad. J. Bot. 52: 1705. 1974.

Notes: Upadhyay (1981) treated *O. coronatum* as synonym of *O. tenellum*, but this was rejected by Hutchison & Reid (1988) because of differences in the ascospore shape. Our data support those of Villarreal *et al.* (2005) and De Beer & Wingfield (2013) that separated the two species. These species group together with *O. nigricarpum*, *O. rostricornatum* and *O. tenellum* in Lineage D (Fig. 1), at present referred to as the *O. tenellum* complex (De Beer & Wingfield 2013). All the species in this complex differ from those in *Sporothrix* s. str. in that they have CAL intron 5, which is lacking in true *Sporothrix* spp. (Table 2). The generic status of all species in the *O. tenellum* complex should be reconsidered because the complex grouped distinct from *Ophiostoma* s. str. and other genera in the *Ophiostomatales* (Fig. 1).

3. ***Ophiostoma grande*** Samuels & E. Müll., Sydowia 31: 176. 1978.

Notes: This species grouped with *O. ambrosium* in a lineage distinct from *Sporothrix* in the study of De Beer & Wingfield (2013). The *O. ambrosium* sequence was not included in our

analyses (see above), but *O. grande* formed a lineage (B, Fig. 1) distinct from *Sporothrix* and all other genera in our analyses. We could not amplify the *BT* gene region for this isolate, but its *CAL* intron arrangement was similar to that of *S. brunneoviolacea*, and thus distinct from all other *Sporothrix* spp. (Table 2).

4. ***Ophiostoma grandicarpum*** (Kowalski & Butin) Rulamort, Bull. Soc. Bot. Centre-Ouest, n.s. 21: 511. 1990. [as '*grandicarpa*']  
*Basionym*: *Ceratocystis grandicarpa* Kowalski & Butin, J. Phytopathol. 124: 243. 1989.

*Notes*: Kowalski & Butin (1989) reported two synasexual morphs in their cultures of this species, but according to Seifert *et al.* (1993), these appear to represent the noncatenate and catenate forms of a sporothrix-like asexual morph. The LSU sequence of the ex-type isolate of this species, together with *O. microsporum*, form a lineage of uncertain generic affiliation in the *Ophiostomatales* (Lineage A, Fig. 1), distinct from *Sporothrix* s. str. This supports the unique placement of the species by De Beer & Wingfield (2013) based on ITS. The *BT* sequence was too divergent to include in our analyses, but the intron composition (3/-/5) reflected those of many *Sporothrix* spp. as well as other *Ophiostomatales* (Table 2).

5. ***Ophiostoma longicollum*** Masuya, Mycoscience 39: 349. 1998.

*Notes*: The morphology of this species from *Quercus* infested by *Platypus quercivorus* in Japan suggests a relatedness with species such as *S. stenoceras* or *O. nigricarpum*. Sequence data are needed to confirm its correct phylogenetic placement.

6. ***Ophiostoma megalobrunneum*** (R.W. Davidson & Toole) de Hoog & Scheffer, Mycologia 76: 297. 1984.  
*Basionym*: *Ceratocystis megalobrunnea* R.W. Davidson & Toole, Mycologia 56: 796. 1964.

*Notes*: This species was isolated from oak sapwood in the USA. Ascospore and asexual morph morphology suggest that this might be a species of *Sporothrix*, but it should be re-examined and sequenced to confirm its placement.

7. ***Ophiostoma microsporum*** Arx, Antonie van Leeuwenhoek 18: 211. 1952.  
*Synonyms*: *Ceratostomella microspora* R.W. Davidson, Mycologia 34: 650. 1942. [*nom. illegit.*, later homonym for *Cs. microspora* Ellis & Everh.]  
*Ceratocystis perparvispora* J. Hunt, Lloydia 19: 46. 1956. [superfluous *nom. nov.*]  
*Ceratocystis microspora* (R.W. Davidson) R.W. Davidson & Aoshima, Ph.D. thesis, University of Tokyo: 20. 1965 [*nom. inval.*]  
*Ceratocystis microspora* (Arx) R.W. Davidson, J. Col.-Wyom. Acad. Sci. 6: 16. 1969.

*Notes*: De Beer *et al.* (2013) discussed the confusing taxonomic history of this species. De Beer & Wingfield included a short LSU sequence for isolate CBS 412.77 generated by Hausner *et al.* (1993b). Our LSU sequence of the ex-neotype isolate (CBS 440.69 = CMW 17152) designated by Davidson &

Kuhlman (1978), is identical to the sequence of Hausner *et al.* (1993b). It groups with *O. grandicarpum* in Lineage A (Fig. 1), distinct from *Sporothrix* and all other genera and was thus not included in the other analyses. The name *O. microsporum* should not be confused with *Leptographium microsporum* R.W. Davidson, neither with *Ceratostomella microspora* (De Beer *et al.* 2013).

8. ***Ophiostoma nigricarpum*** (R.W. Davidson) de Hoog, Stud. Mycol. 7: 62. 1974. [as '*nigrocarpum*']  
*Basionym*: *Ceratocystis nigrocarpa* R.W. Davidson, Mycopath. Mycol. Appl. 28: 276. 1966.

*Notes*: De Beer *et al.* (2003) treated several isolates of *O. abietinum* incorrectly as *O. nigricarpum*. Aghayeva *et al.* (2004) showed that the ex-type isolate of *O. nigricarpum* is distinct from *O. abietinum*. *Ophiostoma nigricarpum* forms part of the *O. tenellum* complex (Lineage D, Fig. 1) (see Notes under *O. coronatum*).

9. ***Ophiostoma noisomeae*** Musvuugwa *et al.*, Antonie van Leeuwenhoek 109: 887. 2016.

*Notes*: Musvuugwa *et al.* (2016) recently described this species from wood and bark of *Rapanea* in South Africa, and recognised that the species grouped outside of *Sporothrix*, *Ophiostoma* s. str. and other genera in the *Ophiostomatales*, similar to its placement in our LSU tree (Lineage C, Fig. 1). However, they did not consider this to be sufficient evidence to establish a distinct, monotypic genus. The *BT* intron composition of *O. noisomeae* is 3/4/5, while that of *Sporothrix* is 3/-/5 or -/-/5 (Table 2). The group served as a convenient outgroup in our analyses (Figs 1–4), but its generic status should be reconsidered.

10. ***Ophiostoma persicinum*** Govi & Di Caro, Ann. Speriment. Agraria, n.s. 7: 1644. 1953.

*Notes*: The morphology of this species from peach tree roots in Italy suggests that it belongs in *Sporothrix* s. str. We could not locate type material for this species and recommend neotypification to enable generic placement based on DNA sequence data.

11. ***Ophiostoma rostrocoronatum*** (R.W. Davidson & Eslyn) de Hoog & Scheffer, Mycologia 76: 297. 1984.  
*Basionym*: *Ceratocystis rostrocoronata* R.W. Davidson & Eslyn. In Eslyn & Davidson, Mem. N.Y. Bot. Gard. 28: 50. 1976.

*Notes*: An ITS sequence produced by Jacobs *et al.* (2003) of the same isolate (CBS 434.77) included in our analyses, grouped with *O. narcissi* in the phylogenies of De Beer & Wingfield (2013). However, based on the four genes sequenced in the present study (Fig. 1, Table 1) and morphology, *O. rostrocoronatum* forms part of the *O. tenellum* complex (De Beer & Wingfield 2013), designated as Lineage D in our analyses (Fig. 1). See note under *O. coronatum*.

12. ***Ophiostoma tenellum*** (R.W. Davidson) M. Villarreal, Mycotaxon 92: 263. 2005.

*Basionym:* *Ceratocystis tenella* R.W. Davidson, Mycologia 50: 666. 1958.

*Synonym:* *Ceratocystis capitata* H.D. Griffin, Can. J. Bot. 46: 699. 1968.

*Notes:* The name-bearing species of the *O. tenellum* complex (Lineage D, Fig. 1) as defined by De Beer & Wingfield (2013). See Note under *O. coronatum*. *Ceratocystis capitata* was treated as a distinct species by Olchowecki & Reid (1974), but suggested to be a synonym of *O. tenellum* by Upadhyay (1981) and listed as such by Villarreal *et al.* (2005) and De Beer *et al.* (2013). The synonymy should be reconsidered.

**13. *Ophiostoma valdivianum*** (Butin) Rulamort, Bull. Soc. Bot. Centre-Ouest, N.S. 17: 192. 1986. [as '*valdiviana*']

*Basionym:* *Ceratocystis valdiviana* Butin. In Butin & Aquilar, Phytopathol. Z. 109: 86. 1984.

*Synonyms:* *Ophiostoma valdivianum* (Butin) T.C. Harr., Mycotaxon 28: 42. 1987. [*nom. illegit.*, Art. 52.1]

*Leptographium valdivianum* Rulamort, Bull. Soc. Bot. Centre-Ouest, N.S. 17: 192. 1986.

*Notes:* In our analyses, the ex-type isolate forms part of Group I in *Sporothrix* as defined in the present study (Figs 2–4). However, in the original description both a *Sporothrix* and *Verticicladiella* asexual morph were described and illustrated. De Rulamort (1986) described the latter morph as *Leptographium valdivianum* from the holotype of *C. valdiviana* (Butin & Aquilar 1984). The leptographium-like asexual morph does not correspond with any other species in *Sporothrix* and was not observed in the ex-type isolate (Table 1) included in the present study. We thus recommend that this isolate should be compared with the holotype in ZT (Zürich, Switzerland) before a final decision is made on the generic placement of the species.

**14. *Sporothrix foliorum*** J.J. Taylor, Mycologia 62: 809. 1970.

*Notes:* Weijman & de Hoog (1985) and de Hoog (1993) treated this species from cabbage leaves in France in *Sporothrix* section *Farinosa*. Species in this section were very distinct from *S. schenckii* and other ophiostomatalean spp., suggesting that this taxon belongs in a non-ophiostomatalean genus. Although the ITS sequence of the ex-type (CBS 326.37) groups between some of the basal lineages in the study of Zhang *et al.* (2015) and blasts to other species of *Ophiostomatales*, the *CAL*, *TEF1* and *TEF3* sequences in the same study clearly shows that this species does not belong in *Sporothrix*. Sequence data for a more conserved gene region such as the LSU would be needed to resolve its generic placement.

**15. *Sporothrix nothofagi*** Gadgil & M.A. Dick, N. Z. J. For. Sci. 34: 318. 2004.

*Notes:* A LSU sequence of the ex-type isolate placed this species peripheral to the *R. lauricola*–*R. sulphurea* species complexes in *Leptographium* s. lat. (Fig. 1) (not close to *Raffaelea* s. str.). This should not be surprising because the fungus is associated with galleries of three native ambrosia beetles infesting *Nothofagus* trees in New Zealand (Gadgil & Dick 2004). The appropriate generic placement of this species should be explored further and it should not be confused with *O. nothofagi* (now *Sporothrix dombeyi*, see above under *Sporothrix*).

## SPOROTHRIX SPP. AND SPECIES WITH SPOROTHRIX-LIKE ASEQUAL MORPHS, BUT OF UNCERTAIN GENERIC OR ORDINAL PLACEMENT

**1. *Ophiostoma roraimense*** Samuels & E. Müll., Sydowia 31: 173. 1978.

*Notes:* LSU and SSU data produced by Hausner *et al.* (1993b) for the ex-type isolate (CBS 351.78) of *O. roraimense* does not group with either the *Ophiostomatales* or *Microascales*. The sequences of *O. roraimense* from the study by Hausner *et al.* (1993b) are not available from GenBank. De Beer & Wingfield (2013) thus retyped the short LSU sequence for the ex-type isolate (CBS 351.78) from the Hausner *et al.* (1993b) paper, and found it had high similarity to several *Pseudozyma* isolates (*Ustilaginales*) in GenBank. Furthermore, the sporodochia with septate conidia (Samuels & Müller 1978) set this species apart from all known species in the *Ophiostomatales*. Since it is possible that the ex-type isolates were contaminated by a *Pseudozyma* sp., we recommend re-examination of the holotype and/or ex-type culture to confirm the generic and ordinal placement of this species.

**2. *Sphaeronema epiglaeum*** Berk. & M.A. Curtis, Grevillea 2: 84. 1873.

*Notes:* *Sphaeronema epiglaeum* from *Tremella* fruiting bodies in the USA was considered a synonym of *O. epiglaeum* from the same host in Argentina according to Guererro (1971). de Hoog (1974) suggested the two species were distinct based on the size of the perithecia, but because he could not find ascospores on the type material from Berkeley, he did not refer *S. epiglaeum* to a more appropriate genus. The name is valid and should be reconsidered if DNA sequences from the type or fresh material can be obtained.

**3. *Sporothrix alba*** (Petch) de Hoog, Stud. Mycol. 7: 22. 1974.  
*Basionym:* *Sporotrichum album* Petch, Trans. Br. mycol. Soc. 11: 262. 1926.

*Notes:* No culture is available for this species from a *Cordyceps* fruiting body on an insect in Sri Lanka (de Hoog 1974). de Hoog (1993) suggested a “clavicipitalean relationship”. The type should be reconsidered and compared with entomopathogenic species such as *Beauveria* (*Cordycipitaceae*, *Hypocreales*) to confirm its generic placement.

**4. *Sporothrix angkangensis*** M.Z. Fan *et al.*, Acta Mycol. Sinica 9: 137. 1990.

*Notes:* This valid species from the moth *Erranis dira* (Geometridae) in China is well-illustrated in the protologue, but its placement in the *Ophiostomatales* needs to be confirmed with DNA sequences. It is more likely affiliated with the *Cordycipitaceae*.

**5. *Sporothrix chondracis*** B. Huang, M.Z. Fan & Z.Z. Li, Mycosystema 16: 88. 1997.

*Notes:* Although the origin of this species from a cotton grasshopper in China is unusual, the illustrations in the protologue suggest that it is a true *Sporothrix* species. However, its



placement in the *Ophiostomatales* needs to be confirmed with DNA sequences, as it possibly belongs in the *Cordycipitaceae*.

6. *Sporothrix echinospora* (Deighton & Piroz.) Katum., *Bull. Faculty of Agriculture, Yamaguchi University* 35: 108. 1987. *Basionym: Calcarisporium echinosporum* Deighton & Piroz., *Mycol. Pap.* 128: 101. 1972.

*Notes:* This species originates from *Meliola* fruiting bodies in Ghana and was described as a hyperparasite. It produces hyaline and pigmented conidia similar to species like *S. inflata* and *S. brunneoviolacea*. Its generic placement should be confirmed but the holotype could not be located.

7. *Sporothrix ghanensis* de Hoog & H.C. Evans, *Stud. Mycol.* 7: 27. 1974.

*Note:* de Hoog (1993) suggested a "clavicipitalean relationship" for this species from spider eggs in Ghana, but this should be confirmed with sequences from the ex-type.

8. *Sporothrix globuligera* K. Matsush. & Matsush., *Matsush. Mycol. Mem.* 8: 52. 1995.

*Note:* The holotype (Kobe MFC-4m837) of this species from soil should be investigated to determine its appropriate generic placement.

9. *Sporothrix insectorum* de Hoog & H.C. Evans, *Stud. Mycol.* 7: 25. 1974.

*Notes:* This species was isolated from insects in Ghana. de Hoog (1993) suggested a "clavicipitalean relationship". Sequences of *S. insectorum* should be compared with species of *Beauveria* to make an accurate generic placement in the *Cordycipitaceae*. Based on information in NCBI GenBank, the full genome sequence of this species is being determined, but data are not yet available online.

10. *Sporothrix inusitatiramosa* H.Z. Kong, *Acta Mycol. Sin.* 10: 129. 1991.

*Notes:* The ex-type culture of this species from wood in China produced an LSU sequence 100% identical to that of *Clonostachys rosea*. However, the illustrations of the conidiogenous cells in the protologue do not resemble those of *Clonostachys*. The culture should be compared with the holotype to determine whether it still represents the same material, as it was most likely contaminated/parasitized by *C. rosea*.

11. *Sporothrix isarioides* (Petch) de Hoog, *Stud. Mycol.* 7: 22. 1974.

*Basionym: Sporotrichum isarioides* Petch, *Trans. Br. mycol. Soc.* 16: 58. 1931.

*Notes:* As with *S. alba*, this species was found on a *Cordyceps* fruiting body on an insect in Sri Lanka (de Hoog 1974). No culture is available but de Hoog (1974) designated a lectotype and suggested some synonyms not listed here. de Hoog (1993) suggested a "clavicipitalean relationship". The lectotype should be re-investigated carefully and compared with *Beauveria* and

similar entomopathogenic species in the *Cordycipitaceae* to confirm its generic placement.

12. *Sporothrix phellini* G.R.W. Arnold, *Feddes Repert. Spec. Nov. Regni Veg.* 98: 354. 1987.

*Notes:* This species was isolated from a *Phellinus* fruiting body in Cuba. de Hoog (1993) suggested that *S. phellini* might belong with the cordicipitalean *Sporothrix* spp. because it seemingly prefers a chitinous substrate. Several true *Sporothrix* spp. have also been isolated from basidiocarps (Tables 1 and 2), so it is possible that this species belongs in *Sporothrix*, although its septate conidia suggest otherwise.

13. *Sporothrix ramosissima* Arnaud ex de Hoog, *Stud. Mycol.* 7: 28. 1974.

*Basionym: Gonatobotrys ramosissima* Arnaud, *Bull. trimest. Soc. mycol. Fr.* 68: 187. 1952. [*nom. inval.*, Art. 36.1].

*Notes:* This species was isolated from moist wood. It differs morphologically from other *Sporothrix* spp. in that it produces branched conidiogenous cells (de Hoog 1974). Weijman & de Hoog (1985) and de Hoog (1993) treated this species in *Sporothrix* section *Farinosa* based on biochemical characters, which were very distinct from those of *S. schenckii* and other ophiostomatalean spp.

14. *Sporothrix ranii* Moustafa, *Persoonia* 11: 392. 1981.

*Note:* Weijman & de Hoog (1985) and de Hoog (1993) treated this species in *Sporothrix* section *Farinosa* based on biochemical characters that distinguished it from *S. schenckii* and other ophiostomatalean species.

15. *Sporothrix sclerotiali* de Hoog, *Persoonia* 10: 64. 1978.

*Note:* This species from the roots of *Lolium perenne* in the Netherlands was treated by Weijman & de Hoog (1985) and de Hoog (1993) in *Sporothrix* section *Farinosa* (see *S. ramosissima*).

16. *Sporothrix setiphila* (Deighton & Piroz.) de Hoog, *Stud. Mycol.* 7: 32. 1974.

*Basionym: Calcarisporium setiphilum* Deighton & Piroz., *Mycol. Pap.* 128: 100. 1972.

*Notes:* This species was found overgrowing a *Meliola* fruiting body (de Hoog 1974). Its holotype (IMI 106418b) should be compared to other fungicolous *Sporothrix* spp., but no culture representing the species exists.

17. *Sporothrix tardilutea* K. Matsush. & Matsush. [as '*tardilutea*'], *Matsush. Mycol. Mem.* 9: 37. 1996.

*Note:* The holotype (Kobe 5T003) of this species from a decaying leaf should be investigated to determine its appropriate generic placement.

18. *Sporothrix vizei* (Berk. & Broome) de Hoog, *Persoonia* 10: 66. 1978.

*Basionym: Verticillium vizei* Berk. & Broome. In Vize, *Microfung. exsicc.*: no. 247. 1880.



Notes: This species from sori on ferns was considered as possibly related to the *Cordycipitaceae* by de Hoog (1993). Its septate conidia and branching conidiophores do not resemble any species in *Sporothrix* s. str.

## SPOROTHRIX SPECIES EXCLUDED FROM THE OPHIOSTOMALES

1. *Sporothrix catenata* de Hoog & Constant., Antonie van Leeuwenhoek 47: 367. 1981.

Notes: The LSU sequence of the ex-type isolate (CBS 215.79) produced in this study is identical to that of *Stephanoascus ciferrii*, currently treated as a synonym of *Trichomonascus ciferrii* (*Trichomonascaceae*, *Saccharomycetales*) (Kurtzman & Robnett 2007). This confirms the synonymy of *S. catenata* with *St. ciferrii* suggested by de Hoog & Constantinescu (1981) based on mating compatibility. The ITS, *BT* and *CAL* sequences of another isolate (CBS 461.81) labelled as *S. catenata* 2 from the nail of a man in the Netherlands, are all virtually identical to the ex-type isolate of *S. nivea* (Figs 2–4), which is currently treated as a synonym of *S. pallida*. The latter isolate should thus be relabelled as *S. pallida*.

2. *Sporothrix cyanescens* de Hoog & G.A. de Vries, Antonie van Leeuwenhoek 39: 515. 1973.

Note: Currently treated as *Quambalaria cyanescens* (*Microstromatales*, *Ustilaginomycetes*) (De Beer et al. 2006).

3. *Sporothrix cylindrospora* Hol.-Jech., Eesti NSV Tead. Akad. Toim., Biol. seer 29: 144. 1980.

Notes: The protologue of this species from *Pinus sibirica* in Turkmenistan could not be obtained for the present study. However, de Hoog et al. (1985) and Weijman & de Hoog (1985) studied the type specimen of *S. cylindrospora* and suggested it is similar to *S. luteoalba* (see below), a basidiomycete currently treated in *Cerinosterus* (Moore 1987).

4. *Sporothrix eucalypti* M.J. Wingf., et al., Mycopathologia 123: 160. 1993.

Note: A basidiomycete incorrectly described in *Sporothrix* and now known as *Quambalaria eucalypti* (*Microstromatales*, *Ustilaginomycetes*) (De Beer et al. 2006).

5. *Sporothrix flocculosa* Traquair, L.A. Shaw & Jarvis, Canad. J. Bot. 66: 927. 1988.

Note: *Sporothrix flocculosa* was previously considered the anamorph of *Pseudozyma flocculosa* in the *Ustilaginales* (Boekhout 1995), and is thus treated as a synonym of this species under the Melbourne Code.

6. *Sporothrix fungorum* de Hoog & G.A. de Vries, Antonie van Leeuwenhoek 39: 518. 1973.

Notes: The ex-type isolate of this species produces asci with ascospores in yeast-like cultures, and it was thus suggested to be a synonym of *Trichomonascus farinosus* (Traquair et al.

1988). Weijman & de Hoog (1985) and de Hoog (1993) treated *S. fungorum* in *Sporothrix* section *Farinosa*. The LSU sequence of the ex-type of *S. fungorum* (Table 1) obtained in the present study showed 95% similarity with its closest match in Genbank, the ex-type of *T. farinosus* (DQ442685). The closest match to the ITS sequence of *S. fungorum* was that of the ex-type isolate of *Blastobotrys nivea* (NR\_077180) with 77% similarity. No ITS data were available for *T. farinosus*, but our results suggest that *S. fungorum* represents a distinct species of *Trichomonascus* as defined by Kurtzman & Robnett (2007). However, further phylogenetic analyses including sequences of more gene regions and species belonging to the *Trichomonascaceae* (*Saccharomycetales*) (Kurtzman & Sugiyama 2015) should be done to confirm the generic placement of *S. fungorum* before a new combination is provided for the name.

7. *Sporothrix luteoalba* de Hoog, Stud. Mycol. 7: 65. 1974.

Note: This species is currently treated as *Cerinosterus luteoalbus* in the *Dacrymycetales* (Moore 1987, Middelhoven et al. 2000).

8. *Sporothrix pitereka* (J. Walker & Bertus) U. Braun. In Braun, Monogr. *Cercospora*, *Ramularia* Allied Genera 2: 416. 1998.

Basionym: *Ramularia pitereka* J. Walker & Bertus, Proc. Linn. Soc. N.S.W. 96(2): 108. 1971.

Note: Currently treated as *Quambalaria pitereka* (*Microstromatales*, *Ustilaginomycetes*) (De Beer et al. 2006).

9. *Sporothrix pusilla* U. Braun & Crous. In Braun, Monogr. *Cercospora*, *Ramularia* Allied Genera 2: 418. 1998.

Note: A basidiomycete now treated as *Quambalaria pusilla* (*Microstromatales*, *Ustilaginomycetes*) (De Beer et al. 2006).

10. *Sporothrix rectidentata* (Matsush.) de Hoog, Persoonia 10: 64. 1978.

Basionym: *Tritirachium rectidentatum* Matsush., Icon. microfung. Matsush. lect. (Kobe): 160. 1975.

Note: This species from forest soil in Japan is currently treated as *Engyodontium rectidentatum* (Gams et al. 1984, Tsang et al. 2016).

11. *Sporothrix rugulosa* Traquair et al., Canad. J. Bot. 66: 929. 1988.

Note: *Sporothrix rugulosa* is the asexual morph of *Pseudozyma rugulosa* (= *Stephanoascus rugulosus*) in the *Ustilaginales* (Boekhout 1995). Under the Melbourne Code it should be listed as a synonym of *Ps. rugulosa*.

12. *Sporothrix sanguinea* C. Ramírez ex J.J. Taylor, Mycologia 69: 651. 1977.

Note: This species from tanning liquors in France is currently treated as *Hyphozyma sanguinea* (de Hoog & Smith 1981).

13. *Sporothrix tuberi* Fontana & Bonfante, Allionia 17: 12. 1971. [*nom. inval.*, Art. 37.1] [as 'tuberum']

Note: de Hoog (1974) validated this species but treated it in the Xylariales as *Nodulisporium tuberculatum*.

## DISCUSSION

Results of the phylogenetic analyses in this study confirmed that species with sporothrix-like asexual morphs do not constitute a monophyletic lineage in the *Ophiostomatales*. The majority of these species group together with *S. schenckii* and the other human pathogenic species in a well-supported lineage that we recognise as the genus *Sporothrix*. This is distinct from *Ophiostoma* s. str. that includes the type for that genus, *O. piliferum*. *Sporothrix*, for which the previous description that was based only on asexual fungi (de Hoog 1974) has been redefined in line with the one fungus one name principles to accommodate species with known sexual states. Our analyses also revealed six well-supported species complexes in the genus.

The newly defined *Sporothrix* includes 51 species. The names for 23 of these species, including the four major human and animal pathogens causing sporotrichosis, remain unchanged. Twenty-six species, previously treated in *Ophiostoma* or *Ceratocystis*, were provided with new combinations in *Sporothrix*. An additional two species, *C. gossypina* var. *robusta* (now *S. rossii*) and *O. nothofagi* (now *S. dombeyi*), received new names (*nom. nov.*) because their epithets would have resulted in illegitimate later homonyms of existing names. None of the 28 changed names are of economically or medically important species. The separation of *Sporothrix* and *Ophiostoma* also implies that the names of several important tree pathogens (e.g. *O. ulmi* and *O. novo-ulmi*) and economically important wood-staining fungi (e.g. *O. piceae* and *O. quercus*) will remain unchanged in *Ophiostoma*.

All species of the newly defined *Sporothrix* share some morphological, ecological and genetic characters that set them apart from other genera and lineages in the *Ophiostomatales* (Table 2). Apart from the fact that they all produce sporothrix-like asexual morphs, they mostly have hyaline to white, smooth, appressed cultures, sometimes becoming grey or brown with age. The sporothrix-like species in *Ophiostoma* s. str., most notably *O. piliferum* and species in the *O. pluriannulatum* complex, produce cultures that are initially white with masses of fluffy aerial mycelium producing conidia, but soon develop dark grey, brown or black pigmentation in the medium, visible when cultures are viewed from below (Upadhyay 1981).

Species in the *Ophiostomatales*, and especially genera such as *Leptographium* s. lat. (Harrington & Cobb 1988, Jacobs & Wingfield 2001, Linnakoski et al. 2012, De Beer & Wingfield 2013), *Ceratocystiopsis* (Upadhyay 1981, Plattner et al. 2009), *Ophiostoma* s. str. (Upadhyay 1981, De Beer & Wingfield 2013) and *Graphilbum* (De Beer & Wingfield 2013) are known primarily as associates of conifer-infesting bark beetles. Some smaller lineages are exceptions in this regard: the *O. ulmi* complex in *Ophiostoma* s. str. and *Fragosphaeria* are staining fungi of hardwoods, while *Raffaelea* s. str. and the other *Raffaelea* lineages are strictly associated with ambrosia beetles infesting both hardwoods and conifers (De Beer & Wingfield 2013). In contrast, *Sporothrix* (Table 2), includes human and animal pathogens, several species from soil, and some from hardwoods and the fruiting bodies of basidiomycetes. Nine species were described

from infructescences of *Proteaceae* native to southern Africa, of which five are known to be associated with hyperphoretic mites (Roets et al. 2008, 2009, 2013). Only eight species in the newly defined *Sporothrix* are associated with conifer-infesting bark beetles. Interestingly, five of these, *S. abietina*, *S. aurorae*, *S. cantabriensis*, *S. euskadiensis*, and *S. nebularis* are associated specifically with root-infesting beetles (Table 1).

Geographically there are also some patterns in the *Ophiostomatales* that generally correspond to the host associations described above. By far the majority of species have been reported from the extensive native conifer forests of North America, Europe and Asia (Hunt 1956, Griffin 1968, Olchoweki & Reid 1974, Upadhyay 1981, Jacobs & Wingfield 2001, Plattner et al. 2009, Linnakoski et al. 2010, 2012). The ophiostomatalean species reported from conifers in the Southern Hemisphere are almost exclusively found associated with introduced bark beetles on non-native pine species grown in plantations (Zhou et al. 2004, 2006, Thwaites et al. 2005). Twenty-four species of *Sporothrix* have been reported from Africa, 11 from South America, five from Australasia, two from Central America, nine from North America, 18 from Europe, and eight from Asia (Table 2). This could reflect an African sampling bias, but *Sporothrix* generally appears to have a broader Southern Hemisphere presence than other genera in the *Ophiostomatales*.

The delineation of *Sporothrix* as a discrete genus, supported by phylogenetic data for three of the gene regions (ITS, *BT* and *CAL*), made it possible to recognise six well-supported species complexes or clades, as well as some smaller emerging lineages in the genus. Central to the genus is the **Pathogenic Clade** (Figs 2–4), typified by *S. schenckii*, one of only four species in the *Ophiostomatales* regularly identified as the causal agents of human or animal sporotrichosis (Travassos & Lloyd 1980, Summerbell et al. 1993, Barros et al. 2004, López-Romero et al. 2011, Zhang et al. 2015). These four species, known only from their asexual morphs (Teixeira et al. 2015), consistently formed a well-supported monophyletic lineage in our analyses. They share certain features that are unique to the *Ophiostomatales* (Table 2). Both *S. schenckii* and *S. globosa* have been isolated from humans, animals and soil (Marimon et al. 2007, Rodrigues et al. 2014a, Zhang et al. 2015). Although it is suspected that *S. brasiliensis* also occurs in soil, attempts to isolate it from this substrate have not been successful (Montenegro et al. 2014) and apart from humans and animals, it has been isolated only from house dust (Marimon et al. 2007). The fourth species, *S. luriei*, is known only from a single clinical isolate (Ajello & Kaplan 1969). All four species produce small, pigmented blastoconidia in addition to the more commonly occurring hyaline conidia. This character is shared by only five other *Sporothrix* species, also found in soil (Table 2). The pigmented blastoconidia appear to be an adaptation to survive in the soil, and melanin most probably allows these opportunistic pathogens to overcome human and animal immune systems when implanted through trauma in skin or muscle tissue (Romero-Martinez et al. 2000, Morris-Jones et al. 2003, Madrid et al. 2010b, Teixeira et al. 2010, 2015). Most other species in the *Ophiostomatales* apparently lack this ability, and despite the fact that they are commonly present on freshly cut wood in virtually every sawmill, pulp mill and plantation globally, they very rarely cause disease. Only a few cases of infections in humans by species from the other genera in the *Ophiostomatales* are known, e.g. *O. piceae* (Morelet 1995, Bommer et al. 2009). Four

*Sporothrix* species from other complexes in the genus that are also opportunistic human pathogens are discussed below.

The largest of the six species complexes in *Sporothrix* is the **S. gossypina complex** (Table 2, Figs 2–4). The complex presently includes 12 species, most of which are sexually reproducing and widely distributed in especially Europe and North America. Six of the species, including the first species to be described in the complex, *S. gossypina*, are associated with galleries of conifer-infesting bark beetles. Two of these have been reported widely. *Sporothrix gossypina* was isolated from older galleries of various *Dendroctonus* and *Ips* bark beetles and other bark infesting insects on several different conifers across the USA (Davidson 1971). Similarly, *S. abietina* have been reported from galleries of different pine-infesting bark beetles in Mexico (Marmolejo & Butin 1990, Zhou *et al.* 2004), South Africa (Zhou *et al.* 2006), China (Lu *et al.* 2009), Russia (Linnakoski *et al.* 2010), Canada (Six *et al.* 2011), the USA (Taerum *et al.* 2013), and Poland (Jankowiak & Bilanski 2013). The other four species from pine bark beetles come from single reports: *S. rossi* from the USA (Davidson 1971), *S. aurorae* from South Africa (Zhou *et al.* 2006), and two species from Spain (Romón *et al.* 2014a, 2014b). Interestingly, the *S. gossypina* complex is the only species complex in *Sporothrix*, apart from Lineage G, which includes species associated with conifer-infesting bark beetles. A further three species in the complex are from stained oak (Kowalski & Butin 1989, Aghayeva *et al.* 2004). One is from cankers caused by *Cryphonectria parasitica* on chestnut (Davidson 1978), one is from a hardwood native to South Africa (Musvuugwa *et al.* 2016), and one is from mites on *Protea* infructescences (Roets *et al.* 2008). The species in the complex thus seem to originate from a variety of sources, with almost the only common factor being stained sapwood exposed to arthropods. From our data it is clear that most species in this complex are genetically almost indistinguishable (Figs 2–4), and that the complex needs to be revised based on multigene phylogenies that include several isolates representing each species.

The **S. stenoceras complex** includes six species (Table 2), the best known of which is *S. stenoceras*. It has been isolated especially from hardwoods and soil in various continents (De Beer *et al.* 2003, Novotný & Šrůtka 2004, Musvuugwa *et al.* 2016), while *S. narcissi* comes from flower bulbs (Limber 1950). Four more species from *Protea* infructescences (Roets *et al.* 2013) forms a subclade in the complex (Figs 2–4), but not with enough statistical support to define it at present as a distinct species complex. One of these species, *S. splendens*, has been confirmed to be vectored by mites (Roets *et al.* 2013), and this could suggest that some of the other species in the complex are also mite associates. Only *S. stenoceras* from this complex has been associated with human and animal disease, and this is only in very rare instances (Mariat *et al.* 1968, Rodrigues *et al.* 2015a, 2015b).

At present the **S. inflata complex** (Figs 2–4) contains only *S. dentifunda*, *S. inflata* and *S. guttiformis*. *Sporothrix dentifunda* was isolated from oak in Europe, while the latter two species are from soil in Europe and Malaysia (de Hoog 1974, 1978, Aghayeva *et al.* 2005).

The **S. candida complex** (Figs 2–4) includes five species, all of which were relatively recently described from hardwoods. *Sporothrix candida* is from wounds on *Eucalyptus* trees (Kamgan Nkuekam *et al.* 2012), and *S. rapanae* and *S. itsvo* from inner bark of *Rapanea* trees (Musvuugwa *et al.* 2016), all from South Africa. *Sporothrix aemulophila* and *S. cabralii* are both associated

with ambrosia beetles, respectively from *Xyleborinus aemulus* infesting *Rapanea* in South Africa (Musvuugwa *et al.* 2015), and galleries of a *Gnathotrupes* sp. infesting *Nothofagus* in Argentina (De Errasti *et al.* 2016). The Argentinean fungus is the only species for which a sexual state has not been observed. The possibility that the latter two species might be ambrosial fungi should be explored further, but it is more likely that these fungi are mite-associated “weeds” in the ambrosia galleries.

There are five species from soil in the **S. pallida complex** (Figs 2–4), which has recently been defined by Rodrigues *et al.* (2016). Three of these species, *S. mexicana* (Rodrigues *et al.* 2013, 2015a), *S. chilensis* (Rodrigues *et al.* 2016), and *S. pallida* (Morrison *et al.* 2013), have been reported as rare and opportunistic causal agents for human disease. The remaining three species in the complex have been isolated from proteas in Southern Africa, and two of these are vectored by mites (Roets *et al.* 2013). Only the three taxa from *Protea* in this complex have known sexual states.

Thirteen species included in *Sporothrix* separated in five smaller lineages with little or no statistical support, and which therefore were not defined as species complexes (Table 2, Figs 2–4). These included seven species from hardwoods, two from conifer bark beetle galleries, two from macrofungus fruiting bodies, and one from a *Protea* infructescence. Three of these have also been reported from soil, while one has only been found in soil. These niches correspond with those of species in the other complexes.

Species not included in *Sporothrix* were separated into four groups based on generic or ordinal status. The first group included four species with names in *Sporothrix* that belong in other, well-defined genera of the *Ophiostomatales*. Three of these, *S. pirina*, *S. roboris* and *S. subannulata*, are asexual morphs of known *Ophiostoma* spp. that were previously supplied with binomials, but are now treated as formal synonyms of respectively *O. catonianum*, *O. quercus* and *O. subannulatum* (De Beer *et al.* 2013). The fourth species, *S. lignivora*, has recently been described in the new genus, *Hawksworthiomyces* (De Beer *et al.* 2016). Our data further confirmed that four *Ophiostoma* species with sporothrix-like asexual morphs, all of previously uncertain generic placement, belong in *Ophiostoma* s. str. These include *O. angusticollis*, *O. denticulatum*, *O. macrosporum* and *O. ponderosae*. Many of these species in other genera in the *Ophiostomatales* that produce sporothrix-like asexual morphs, also produce hyalorhinocladia- or synnemata- pesotum-like synasexual morphs.

*Sporothrix foliorum* and *S. nothofagi*, together with 13 *Ophiostoma* spp. that have sporothrix-like asexual morphs, clearly belong in the *Ophiostomatales*, but did not group with confidence in *Sporothrix* or in any of the currently defined genera in the order. Their placement needs to be confirmed with more robust DNA sequence data, including more conserved gene regions appropriate for genus-level resolution.

The ordinal placement of 16 *Sporothrix* spp. and two additional species with sporothrix-like asexual morphs remains uncertain. Although DNA sequences might confirm the placement of some of these species in the *Ophiostomatales*, several were isolated from an anomalous substrate, dead insects. Consequently, de Hoog (1993) suggested that they might be related to insect pathogens in the *Cordycipitaceae*.

Thirteen species previously described in *Sporothrix* have been excluded from the genus and the *Ophiostomatales*. Eight are basidiomycetes in the genera *Quambalaria* (*Microstromatales*,



*Ustilaginomycetes*) (De Beer *et al.* 2006), *Pseudozyma* (*Ustilaginales*, *Ustilaginomycetes*) (Boekhout 1995), and *Cerinosterus* (*Dacrymycetales*, *Dacrymycetes*) (Middelhoven *et al.* 2000). The remaining species belong to ascomycete genera such as *Trichomonascus* and *Blastobotrys* (*Saccharomycetales*, *Saccharomycetes*), *Engyodontium* (*Cordycipitaceae*, *Hypocreales*, *Sordariomycetes*), *Hyphozyma* (*Leotiomycetes*) and *Nodulisporium* (*Xylariales*, *Sordariomycetes*).

Although generic placements could not be resolved for all *Sporothrix* spp. in this study, the separation of *Sporothrix* from *Ophiostoma* represents a major step forward in resolving the taxonomy of the *Ophiostomatales*. Importantly, it has been focused to ensure nomenclatural stability for the economically and medically important species in the order. The appropriate generic placement of several unresolved lineages remains to be determined in a more extensive study including as many taxa as possible in the order. Several more conserved gene regions must be studied. The newly defined complexes in *Sporothrix* shed new light on the evolution of species in the genus. Species concepts and possible synonymies in these complexes should be investigated by including as many isolates as possible of the species considered. Sequences of additional protein-coding gene regions are needed. A key to accomplishing this goal will be the making of new collections representing species for which cultures are not available. Collections of these fungi are also needed from areas of the world where they are poorly known.

## ACKNOWLEDGEMENTS

We are grateful to Dr Hugh Glen for advice with regards to Latinized names, as well as to Runlei Chang, Andres de Errasti, Miranda Erasmus, Tendai Musvuugwa, Gilbert Kamgan Nkuekam, and Mingliang Yin who provided DNA sequences used in this study. We acknowledge funding from the National Research Foundation, members of the Tree Protection Cooperative Programme (TPCP), and the DST/NRF Centre of Excellence in Tree Health Biotechnology (CTHB), South Africa.

## REFERENCES

- Aghayeva DN, Wingfield MJ, De Beer ZW, *et al.* (2004). Two new *Ophiostoma* species with *Sporothrix* anamorphs from Austria and Azerbaijan. *Mycologia* **96**: 866–878.
- Aghayeva DN, Wingfield MJ, Kirisits T, *et al.* (2005). *Ophiostoma dentifundum* sp. nov. from oak in Europe, characterized using molecular phylogenetic data and morphology. *Mycological Research* **109**: 1127–1136.
- Ajello L, Kaplan W (1969). A new variant of *Sporothrix schenckii*. *Mykosen* **12**: 633–644.
- Andrieu S, Biguet J, Massamba S (1971). Etude immunologique comparee de *Sporothrix schenckii* et des souches saprophytes voisines. *Sabouraudia* **9**: 206–209.
- Ansel M, Thibaut M (1970). Une nouvelle Endomycetaceae: *Dolichoascus* nov. gen. Découverte de la reproduction sexuée par asques chez *Sporotrichum schenckii* (Hektoen et Perkins, 1900). *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences* **270**: 2171–2173.
- Bakshi BK (1950). Fungi associated with Ambrosia beetles in Great Britain. *Transactions of the British Mycological Society* **33**: 111–120.
- Barron GL (1968). *The genera of Hyphomycetes from soil*. The Williams and Wilkins Company, New York, USA.
- Barros MBdL, Schubach AdO, do Valle ACF, *et al.* (2004). Cat-transmitted sporotrichosis epidemic in Rio de Janeiro, Brazil: description of a series of cases. *Clinical Infectious Diseases* **38**: 529–535.
- Berbee ML, Taylor JW (1992). 18S Ribosomal RNA gene sequence characters place the pathogen *Sporothrix schenckii* in the genus *Ophiostoma*. *Experimental Mycology* **16**: 87–91.
- Boekhout T (1995). *Pseudozyma* Bandoni emend. Boekhout, a genus for yeast-like anamorphs of Ustilaginales. *Journal of General and Applied Microbiology* **41**: 359–366.
- Bommer M, Hutter M-L, Stilgenbauer S, *et al.* (2009). Fatal *Ophiostoma piceae* infection in a patient with acute lymphoblastic leukaemia. *Journal of Medical Microbiology* **58**: 381–385.
- Butin H, Aquilar AM (1984). Bluestain fungi on *Nothofagus* from Chile – Including two new species of *Ceratocystis* Ellis & Halst. *Phytopathologische Zeitschrift* **109**: 80–89.
- Carmichael JW (1962). *Chrysosporium* and some other aleuriosporic *Hyphomycetes*. *Canadian Journal of Botany* **40**: 1137–1173.
- Castresana J (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* **17**: 540–552.
- Chen M, Zeng J, de Hoog GS, *et al.* (2016). The 'species complex' issue in clinically relevant fungi: a case study in *Scedosporium apiospermum*. *Fungal Biology* **120**: 137–146.
- Constantinescu O, Ryman S (1989). A new *Ophiostoma* on polypores. *Mycotaxon* **34**: 637–642.
- Davidson RW (1942). Some additional species of *Ceratostomella* in the United States. *Mycologia* **34**: 650–662.
- Davidson RW (1971). New species of *Ceratocystis*. *Mycologia* **63**: 5–15.
- Davidson RW (1978). A new species of *Ceratocystis* on *Endothia parasitica* canker of American chestnut. *Mycologia* **70**: 856–858.
- Davidson RW, Kuhlman EG (1978). A species of *Ceratocystis* closely associated with *Endothia* cankers on American chestnut in Eastern United States. *Mycologia* **70**: 853–855.
- Davis DJ (1920). The identity of American and French Sporotrichosis. *University of Wisconsin Studies in Science* **1**: 105–131.
- De Beer ZW, Wingfield MJ (2013). Emerging lineages in the *Ophiostomatales*. In: *The ophiostomatoid fungi: expanding frontiers* (Seifert KA, De Beer ZW, Wingfield MJ, eds), *CBS biodiversity series*. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 21–46.
- De Beer ZW, Harrington TC, Vismar HF, *et al.* (2003). Phylogeny of the *Ophiostoma stenoceras*–*Sporothrix schenckii* complex. *Mycologia* **95**: 434–441.
- De Beer ZW, Begerow D, Bauer R, *et al.* (2006). Phylogeny of the *Quambalariaeaceae* fam. nov., including important *Eucalyptus* pathogens in South Africa and Australia. *Studies in Mycology* **55**: 289–298.
- De Beer ZW, Seifert KA, Wingfield MJ (2013). A nomenclator for ophiostomatoid genera and species in the *Ophiostomatales* and *Microascales*. In: *The ophiostomatoid fungi: expanding frontiers* (Seifert KA, De Beer ZW, Wingfield MJ, eds), *CBS biodiversity series*. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 245–322.
- De Beer ZW, Marincowitz S, Duong TA, *et al.* (2016). *Hawksworthiomyces* gen. nov. (*Ophiostomatales*), illustrates the urgency for a decision on how to name novel taxa known only from environmental nucleic acid sequences (ENAS). *Fungal Biology*. <http://dx.doi.org/10.1016/j.funbio.2016.07.004>.
- De Beurmann L, Gougerot H (1911). Les *Sporotrichum* pathogènes. Classification botanique. *Archives de Parasitologie* **15**: 5–109.
- De Errasti A, De Beer ZW, Coetzee MPA, *et al.* (2016). Three new species of *Ophiostomatales* from *Nothofagus* in Patagonia. *Mycological Progress* **15**: 17.
- de Hoog GS (1974). The genera *Blastobotrys*, *Sporothrix*, *Calcarisporium* and *Calcarisporiella* gen. nov. *Studies in Mycology* **7**: 1–84.
- de Hoog GS (1978). Notes on some fungicolous *Hyphomycetes* and their relatives. *Persoonia* **10**: 33–81.
- de Hoog GS (1993). *Sporothrix*-like anamorphs of *Ophiostoma* species and other fungi. In: *Ceratocystis and Ophiostoma: taxonomy, ecology and pathogenicity* (Wingfield MJ, Seifert KA, Webber J, eds). APS Press, St. Paul, Minnesota: 53–60.
- de Hoog GS, Constantinescu O (1981). A new species of *Sporothrix* from calf skin. *Antonie van Leeuwenhoek* **47**: 367–370.
- de Hoog GS, Smith M (1981). *Hyphozyma*, a new genus of yeast-like *Hyphomycetes*. *Antonie van Leeuwenhoek* **47**: 339–352.
- de Hoog GS, Rantio-Lehtimäki AH, Smith MT (1985). *Blastobotrys*, *Sporothrix* and *Trichosporiella*: generic delimitation, new species, and a *Stephanoascus* teleomorph. *Antonie van Leeuwenhoek* **51**: 79–109.
- De Meyer EM, De Beer ZW, Summerbell RC, *et al.* (2008). Taxonomy and phylogeny of new wood- and soil-inhabiting *Sporothrix* species in the *Ophiostoma stenoceras*–*Sporothrix schenckii* complex. *Mycologia* **100**: 647–661.
- De Rulamor M (1986). Remarques taxinomiques et nomenclaturales sur quelques micromycètes. *Bulletin de la Société Botanique du Centre-Ouest* **17**: 191–192.



- Dias NM, Lima N, Oliveira MME, et al. (2011). Sporotrichosis caused by *Sporothrix mexicana*, Portugal. *Emerging Infectious Diseases* **17**: 1975–1976.
- Domsch KH, Gams W, Anderson T-H (1980). *Compendium of soil fungi*. Academic Press, London.
- Duong TA, De Beer ZW, Wingfield BD, Wingfield MJ (2012). Phylogeny and taxonomy of species in the *Grosmannia serpens* complex. *Mycologia* **104**: 715–732.
- Gadgil PD, Dick MA (2004). Fungi Silvicolae Novaezelandiae: 5. *New Zealand Journal of Forestry Science* **34**: 316–323.
- Gams W, de Hoog GS, Samson RA, et al. (1984). The hyphomycete genus *Engyodontium*: a link between *Verticillium* and *Aphanocladium*. *Persoonia* **12**: 135–147.
- Gardes M, Bruns TD (1993). ITS primers with enhanced specificity for basidiomycetes – Application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**: 113–118.
- Georgescu CC, Teodoru I, Badea M (1948). Uscarea in massa a stejarului. Ciupere de alteratie cromatica parazitara a lemnului de stejar. *Analele Institutului de Cercetari Forestiere al României* **11**: 185–217.
- Glass NL, Donaldson GC (1995). Development of primer sets designed for use with the PCR to amplify conserved genes from filamentous Ascomycetes. *Applied and Environmental Microbiology* **61**: 1323–1330.
- Goidanich G (1935). Una nuova specie di "Ophiostoma" vivente sul pero ed alcune osservazioni sull'esatta posizione sistematica della forma ascofora e delle forme metagenetiche del genere. *Bolletino della Stazione di Patologia Vegetale di Roma* **15**: 122–168.
- Griffin HD (1968). The genus *Ceratocystis* in Ontario. *Canadian Journal of Botany* **46**: 689–718.
- Grobbelaar J, Aghayeva D, De Beer ZW, et al. (2009). Delimitation of *Ophiostoma quercus* and its synonyms using multiple gene phylogenies. *Mycological Progress* **8**: 221–236.
- Guerrero RT (1971). On the real nature of the "setae" in *Tremella fuciformis*. *Mycologia* **63**: 920–924.
- Gutierrez Galhardo MC, De Oliveira RMZ, Do Valle ACF, et al. (2008). Molecular epidemiology and antifungal susceptibility patterns of *Sporothrix schenckii* isolates from a cat-transmitted epidemic of sporotrichosis in Rio de Janeiro, Brazil. *Medical Mycology* **46**: 141–151.
- Halschlagler E, Kowalski T (2003). *Sporothrix inflata*, a root-inhabiting fungus of *Quercus robur* and *Q. petraea*. *Mycological Progress* **2**: 259–266.
- Harrington TC, Cobb FW (1988). *Leptographium root diseases on conifers*. APS Press, St. Paul, Minnesota.
- Hausner G, Reid J (2003). Notes on *Ceratocystis brunnea* and some other *Ophiostoma* species based on partial ribosomal DNA sequence analysis. *Canadian Journal of Botany* **81**: 865–876.
- Hausner G, Reid J, Klassen GR (1993a). On the phylogeny of *Ophiostoma*, *Ceratocystis* s.s., and *Microascus*, and relationships within *Ophiostoma* based on partial ribosomal DNA sequences. *Canadian Journal of Botany* **71**: 1249–1265.
- Hausner G, Reid J, Klassen GR (1993b). On the subdivision of *Ceratocystis* s.l., based on partial ribosomal DNA sequences. *Canadian Journal of Botany* **71**: 52–63.
- Hausner G, Reid J, Klassen GR (2000). On the phylogeny of members of *Ceratocystis* s.s. and *Ophiostoma* that possess different anamorphic states, with emphasis on the anamorph genes *Leptographium*, based on partial ribosomal DNA sequences. *Canadian Journal of Botany* **78**: 903–916.
- Hawksworth DL (2011). A new dawn for the naming of fungi: impacts of decisions made in Melbourne in July 2011 on the future publication and regulation of fungal names. *Mycologia* **1**: 7–20.
- Hedgcock GG (1906). Studies upon some chromogenic fungi which discolor wood. *Missouri Botanical Garden Annual Report* **17**: 59–114.
- Hektoen L, Perkins CF (1900). Refractory subcutaneous abscesses caused by *Sporothrix schenckii*, a new pathogenic fungus. *Journal of Experimental Medicine* **5**: 77–89.
- Hinds TE, Davidson RW (1975). Two new species of *Ceratocystis*. *Mycologia* **67**: 715–721.
- Hunt J (1956). Taxonomy of the genus *Ceratocystis*. *Lloydia* **19**: 1–58.
- Hutchison LJ, Reid J (1988). Taxonomy of some potential wood-staining fungi from New Zealand. 1. *Ophiostomataceae*. *New Zealand Journal of Botany* **26**: 63–81.
- Jacobs K, Wingfield MJ (2001). *Leptographium* species: tree pathogens, insect associates, and agents of blue-stain. APS Press, St. Paul, Minnesota, USA.
- Jacobs K, Seifert KA, Harrison KJ, et al. (2003). Identity and phylogenetic relationships of ophiostomatoid fungi associated with invasive and native *Tetropium* species (Coleoptera: Cerambycidae) in Atlantic Canada. *Canadian Journal of Botany* **81**: 316–329.
- Jankowiak R, Bilanski P (2013). Diversity of ophiostomatoid fungi associated with the large pine weevil, *Hylobius abietis*, and infested Scots pine seedlings in Poland. *Annals of Forest Science* **70**: 391–402.
- Kamgan Nkuekam G, Jacobs K, De Beer ZW, et al. (2008). *Ceratocystis* and *Ophiostoma* species including three new taxa, associated with wounds on native South African trees. *Fungal Diversity* **29**: 37–59.
- Kamgan Nkuekam G, De Beer ZW, Wingfield MJ, Roux J (2012). A diverse assemblage of *Ophiostoma* species, including two new taxa on eucalypt trees in South Africa. *Mycological Progress* **11**: 515–533.
- Katoh K, Standley DM (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780.
- Kowalski T, Butin H (1989). Taxonomie bekannter und neuer *Ceratocystis*-Arten an Eiche (*Quercus robur* L.). *Journal of Phytopathology* **124**: 236–248.
- Kurtzman CP, Robnett CJ (2007). Multigene phylogenetic analysis of the *Trichomonascus*, *Wickerhamiella* and *Zygoascus* yeast clades, and the proposal of *Sugiyamaella* gen. nov. and 14 new species combinations. *FEMS Yeast Research* **7**: 141–151.
- Kurtzman CP, Sugiyama J (2015). 1 Saccharomycotina and Taphrinomycotina: the yeasts and yeastlike fungi of the Ascomycota. In: *Systematics and evolution: Part B* (McLaughlin JD, Spatafora WJ, eds). Springer Berlin Heidelberg, Berlin, Heidelberg: 3–33.
- Lagerberg T, Lundberg G, Melin E (1927). Biological and practical researches into blueing in pine and spruce. *Svenska Skogsvårdsföreningens Tidskrift* **25**: 145–272.
- Limber DP (1950). *Ophiostoma* on *Narcissus* bulbs. *Phytopathology* **40**: 493–496.
- Linnakoski R, De Beer ZW, Rousi M, et al. (2008). Fungi including *Ophiostoma karelicum* sp. nov., associated with *Scolytus ratzeburgi* infesting birch in Finland and Russia. *Mycological Research* **112**: 1475–1488.
- Linnakoski R, De Beer ZW, Ahtainen J, et al. (2010). *Ophiostoma* spp. associated with pine and spruce-infesting bark beetles in Finland and Russia. *Persoonia* **25**: 72–93.
- Linnakoski R, De Beer ZW, Duong TA, et al. (2012). *Grosmannia* and *Leptographium* spp. associated with conifer-infesting bark beetles in Finland and Russia, including *Leptographium taigense* sp. nov. *Antonie van Leeuwenhoek* **102**: 375–399.
- López-Romero E, Reyes-Montes MdR, Pérez-Torres A, et al. (2011). *Sporothrix schenckii* complex and sporotrichosis, an emerging health problem. *Future Microbiology* **6**: 85–102.
- Lu M, Zhou XD, De Beer ZW, et al. (2009). Ophiostomatoid fungi associated with the invasive pine-infesting bark beetle, *Dendroctonus valens*, in China. *Fungal Diversity* **38**: 133–145.
- Madrid H, Cano J, Gené J, et al. (2009). *Sporothrix globosa*, a pathogenic fungus with widespread geographical distribution. *Revista Iberoamericana de Micología* **26**: 18–22.
- Madrid H, Gene J, Cano J, et al. (2010a). *Sporothrix brunneoviolacea* and *Sporothrix dimorphospora*, two new members of the *Ophiostoma stenoceras*–*Sporothrix schenckii* complex. *Mycologia* **102**: 1193–1203.
- Madrid IM, Xavier MO, Mattei AS, et al. (2010b). Role of melanin in the pathogenesis of cutaneous sporotrichosis. *Microbes & Infection* **12**: 162–165.
- Mariat F (1971). Adaptation de *Ceratocystis* a la vie parasitaire chez l'animal — etude de l'acquisition d'un pouvoir pathogene comparable a celui de *Sporothrix schenckii*. *Medical Mycology* **9**: 191–205.
- Mariat F, De Bievre C (1968). Caractères de la croissance et évolution de la teneur en constituants cellulaires des phases levure et filamenteuse de *Sporotrichum schenckii*, champignon dimorphique pathogène pour l'homme. *Annales de l'Institut Pasteur* **115**: 1082–1098.
- Mariat F, Diez E (1971). Nature des spores endogènes de *Sporothrix schenckii* Hektoen et Perkins. Remarques à propos de l'éventuelle forme sexuée de ce champignon. *Comptes rendus hebdomadaires des séances de l'Académie des sciences* **272**: 1075–1077.
- Mariat F, Escudie A, Gaxotte F (1968). Isolement de souches de *Ceratocystis* sp. a la forme conidienne de *Sporotrichum* de cuirs chevelus humains et de poils de rats. Comparaison avec l'espece pathogene *S. schenckii*. *Comptes rendus hebdomadaires des séances de l'Académie des sciences* **267**: 974–976.
- Marimon R, Gene J, Cano J, et al. (2006). Molecular phylogeny of *Sporothrix schenckii*. *Journal of Clinical Microbiology* **44**: 3251–3256.
- Marimon R, Cano J, Gene J, et al. (2007). *Sporothrix brasiliensis*, *S. globosa*, and *S. mexicana*, three new *Sporothrix* species of clinical interest. *Journal of Clinical Microbiology* **45**: 3198–3206.

- Marimon R, Gene J, Cano J, et al. (2008). *Sporothrix luriei*: a rare fungus from clinical origin. *Medical Mycology* **46**: 621–625.
- Marmolejo JG, Butin H (1990). New conifer-inhabiting species of *Ophiostoma* and *Ceratocystiopsis* (Ascomycetes, Microascales) from Mexico. *Sydowia* **42**: 193–199.
- Masuya H, Yamaoka Y, Wingfield MJ (2013). Ophiostomatoid fungi and their associations with bark beetles in Japan. In: *The ophiostomatoid fungi: expanding frontiers* (Seifert KA, De Beer ZW, Wingfield MJ, eds), CBS biodiversity series. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 77–90.
- Mathiesen-Käärik A (1953). Eine Übersicht über die gewöhnlichsten mit Borkenkäfern assoziierten Bläuepilze in Schweden und einige für Schweden neue Bläuepilze. *Meddelanden från Statens Skogsforskningsinstitut* **43**: 1–74.
- McNeill J, Barrie FR, Buck WR, et al. (2012). *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code)*, *Regnum Vegetabile 154*. ARG Gantner Verlag KG, Germany.
- Melin E, Nannfeldt JA (1934). Researches into the blueing of ground wood-pulp. *Svenska Skogsvårdsföreningens Tidskrift* **32**: 397–616.
- Middelhoven WJ, Guého E, de Hoog GS (2000). Phylogenetic position and physiology of *Cerinosterus cyanescens*. *Antonie van Leeuwenhoek* **77**: 313–320.
- Montenegro H, Rodrigues AM, Dias MA, et al. (2014). Feline sporotrichosis due to *Sporothrix brasiliensis*: an emerging animal infection in Sao Paulo, Brazil. *BMC Veterinary Research* **10**: 269.
- Moore RT (1987). Micromorphology of yeasts and yeast-like fungi and its taxonomic implications. *Studies in Mycology* **30**: 203–226.
- Morelet M (1995). II. Travaux scientifiques. Notes de mycologie appliquée. *Annales de la Société des Sciences Naturelles et d'Archéologie de Toulon et du Var* **47**: 89–94.
- Morris-Jones R, Youngchim S, Gomez BL, et al. (2003). Synthesis of melanin-like pigments by *Sporothrix schenckii* in vitro and during mammalian infection. *Infection and Immunity* **71**: 4026–4033.
- Morrison AS, Lockhart SR, Bromley JG, et al. (2013). An environmental *Sporothrix* as a cause of corneal ulcer. *Medical Mycology Case Reports* **2**: 88–90.
- Moustafa AF (1981). A new species of *Sporothrix* from Kuwait. *Persoonia* **11**: 392–394.
- Münch E (1907). Die Blaufäule des Nadelholzes. I–II. *Naturwissenschaftliche Zeitschrift für Forst- und Landwirtschaft* **5**: 531–573.
- Musvuugwa T, De Beer ZW, Duong TA, et al. (2015). New species of Ophiostomatales from Scolytinae and Platypodinae beetles in the Cape Floristic Region, including the discovery of the sexual state of *Raffaella*. *Antonie van Leeuwenhoek* **108**: 933–950.
- Musvuugwa T, De Beer ZW, Duong TA, et al. (2016). Wounds on *Rapanea melanophloeos* provide habitat for a large diversity of Ophiostomatales including four new species. *Antonie van Leeuwenhoek* **109**: 877–894.
- Nicot J, Mariat F (1973). Caractères morphologiques et position systématique de *Sporothrix schenckii*, agent de la sporotrichose humaine. *Mycopathologia et Mycologia Applicata* **49**: 53–65.
- Norvell LL (2011). Fungal nomenclature. 1. Melbourne approves a new code. *Mycotaxon* **116**: 481–490.
- Novotný D, Šrůtka P (2004). *Ophiostoma stenoceras* and *O. grandicarpum* (Ophiostomatales), first records in the Czech Republic. *Czech Mycology* **56**: 19–32.
- O'Donnell K, Cigelnik E (1997). Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are nonorthologous. *Molecular Phylogenetics and Evolution* **7**: 103–116.
- O'Donnell K, Nirenberg H, Aoki T, et al. (2000). A multigene phylogeny of the *Gibberella fujikuroi* species complex: detection of additional phylogenetically distinct species. *Mycoscience* **41**: 61–78.
- Olchowecki A, Reid J (1974). Taxonomy of the genus *Ceratocystis* in Manitoba. *Canadian Journal of Botany* **52**: 1675–1711.
- Oliveira DC, Lopes PGM, Spader TB, et al. (2011). Antifungal susceptibilities of *Sporothrix albicans*, *S. brasiliensis*, and *S. luriei* of the *S. schenckii* complex identified in Brazil. *Journal of Clinical Microbiology* **49**: 3047–3049.
- Plattner A, Kim J-J, Reid J, et al. (2009). Resolving taxonomic and phylogenetic incongruence within species *Ceratocystiopsis minuta*. *Mycologia* **101**: 878–887.
- Robak H (1932). Investigations regarding fungi on Norwegian ground wood pulp and fungal infection at wood pulp mills. *Nyt Magazin for Naturvidenskaberne* **71**: 185–330.
- Rodrigues AM, de Hoog S, De Camargo ZP (2013). Emergence of pathogenicity in the *Sporothrix schenckii* complex. *Medical Mycology* **51**: 405–412.
- Rodrigues AM, Bagagli E, De Camargo ZP, et al. (2014a). *Sporothrix schenckii* sensu stricto isolated from soil in an armadillo's burrow. *Mycopathologia* **177**: 199–206.
- Rodrigues AM, de Hoog G, De Cassia Pires D, et al. (2014b). Genetic diversity and antifungal susceptibility profiles in causative agents of sporotrichosis. *BMC Infectious Diseases* **14**: 219.
- Rodrigues AM, de Hoog GS, De Camargo ZP (2015a). Molecular diagnosis of pathogenic *Sporothrix* species. *PLoS Neglected Tropical Diseases* **9**: e0004190.
- Rodrigues AM, Najafzadeh MJ, de Hoog GS, et al. (2015b). Rapid identification of emerging human-pathogenic *Sporothrix* species with rolling circle amplification. *Frontiers in Microbiology* **6**: 1385.
- Rodrigues AM, Cruz Choappa R, Fernandes GF, et al. (2016). *Sporothrix chilensis* sp. nov. (Ascomycota: Ophiostomatales), a soil-borne agent of human sporotrichosis with mild-pathogenic potential to mammals. *Fungal Biology* **120**: 246–264.
- Roets F, De Beer ZW, Dreyer LL, et al. (2006). Multi-gene phylogeny for *Ophiostoma* spp. reveals two new species from *Protea* infructescences. *Studies in Mycology* **55**: 199–212.
- Roets F, De Beer ZW, Wingfield MJ, et al. (2008). *Ophiostoma gemellus* and *Sporothrix varicibatus* from mites infesting *Protea* infructescences in South Africa. *Mycologia* **100**: 496–510.
- Roets F, Crous PW, Wingfield MJ, et al. (2009). Mite-mediated hyperphoretic dispersal of *Ophiostoma* spp. from the Infructescences of South African *Protea* spp. *Environmental Entomology* **38**: 143–152.
- Roets F, Wingfield BD, De Beer ZW, et al. (2010). Two new *Ophiostoma* species from *Protea caffra* in Zambia. *Persoonia* **24**: 18–28.
- Roets F, Wingfield MJ, Crous PW, et al. (2013). Taxonomy and ecology of ophiostomatoid fungi associated with *Protea* infructescences. In: *The ophiostomatoid fungi: expanding frontiers* (Seifert KA, De Beer ZW, Wingfield MJ, eds), CBS biodiversity series. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 177–187.
- Romeo O, Scordino F, Criseo G (2011). New insight into molecular phylogeny and epidemiology of *Sporothrix schenckii* species complex based on calmodulin-encoding gene analysis of Italian Isolates. *Mycopathologia* **172**: 179–186.
- Romero-Martinez R, Wheeler M, Guerrero-Plata A, et al. (2000). Biosynthesis and functions of melanin in *Sporothrix schenckii*. *Infection and Immunity* **68**: 3696–3703.
- Romón P, De Beer ZW, Fernández M, et al. (2014a). Ophiostomatoid fungi including two new fungal species associated with pine root-feeding beetles in northern Spain. *Antonie van Leeuwenhoek* **106**: 1167–1184.
- Romón P, De Beer ZW, Zhou X, et al. (2014b). Multigene phylogenies of Ophiostomatales associated with Monterey pine bark beetles in Spain reveal three new fungal species. *Mycologia* **106**: 119–132.
- Ronquist F, Huelsenbeck JP (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.
- Samuels GJ, Müller E (1978). Life history studies of Brazilian Ascomycetes 5. Two new species of *Ophiostoma* and their *Sporothrix* anamorphs. *Sydowia* **31**: 169–179.
- Schenck BR (1898). On refractory subcutaneous abscesses caused by a fungus possibly related to the sporotricha. *Bulletin of the Johns Hopkins Hospital* **9**: 286–290.
- Schoch CL, Seifert KA, Huhndorf S (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *PNAS* **109**: 6241–6246.
- Sczerbin-Parfenenko AL (1953). *Rakovye i sosudistye bolezni listvennykh porod*. Goslesbumizdat, Moskva-Leningrad.
- Seifert KA, Wingfield MJ, Kendrick WB (1993). A nomenclator for described species of *Ceratocystis*, *Ophiostoma*, *Ceratocystiopsis*, *Ceratostomella* and *Sphaeronaemella*. In: *Ceratocystis and Ophiostoma: taxonomy, ecology and pathogenicity* (Wingfield MJ, Seifert KA, Webber J, eds). APS Press, St. Paul, Minnesota: 269–287.
- Siemaszko W (1939). Zespoły grzybów towarzyszących kornikom polskim. *Planta Polonica* **7**: 1–54.
- Silvestro D, Michalak I (2012). raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity & Evolution* **12**: 335–337.
- Six D, De Beer ZW, Duong TA, et al. (2011). Fungal associates of the lodgepole pine beetle, *Dendroctonus murrayanae*. *Antonie van Leeuwenhoek* **100**: 231–244.
- Smith MT, Batenburg-Van der Vegte WH (1985). Ultrastructure of septa in *Blastobotrys* and *Sporothrix*. *Antonie van Leeuwenhoek* **51**: 121–128.
- Stafleu FA (1972). International Code of Botanical Nomenclature. Adopted by the Eleventh International Botanical Congress, Seattle, August 1969. *Regnum Vegetabile* **82**: 1–426.

- Stalpers JA (1978). Identification of wood-inhabiting *Aphylophorales* in pure culture. *Studies in Mycology* **16**: 1–248.
- Stamatakis A (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–2690.
- Summerbell RC, Kane J, Krajdien S, *et al.* (1993). Medically important *Sporothrix* species and related ophiostomatoid fungi. In: *Ceratocystis and Ophiostoma: taxonomy, ecology and pathogenicity* (Wingfield MJ, Seifert KA, Webber J, eds). APS Press, St. Paul, Minnesota: 185–192.
- Sydow vH, Sydow P (1919). Mycologische Mitteilungen. *Annales Mycologici* **17**: 33–47.
- Taerum SJ, Duong TA, De Beer ZW, *et al.* (2013). Large shift in symbiont assemblage in the invasive red turpentine beetle. *PLoS One* **8**: e78126.
- Tamura K, Stecher G, Peterson D, *et al.* (2013). MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution* **30**: 2725–2729.
- Taylor JJ (1970). A comparison of some *Ceratocystis* species with *Sporothrix schenckii*. *Mycopathologia* **42**: 233–240.
- Teixeira PA, De Castro RA, Ferreira FR, *et al.* (2010). L-DOPA accessibility in culture medium increases melanin expression and virulence of *Sporothrix schenckii* yeast cells. *Medical Mycology* **48**: 687–695.
- Teixeira MdM, Rodrigues AM, Tsui CKM, *et al.* (2015). Asexual propagation of a virulent clone complex in a human and feline outbreak of sporotrichosis. *Eukaryotic Cell* **14**: 158–169.
- Thibaut M (1972). La forme parfaite du *Sporotrichum schenckii* (Hektoen et Perkins 1900): *Dolichoascus schenckii* Thibaut et Ansel 1970 nov. gen. *Annales de Parasitologie Humaine et Comparee* **47**: 431–441.
- Thwaites JM, Farrell RL, Duncan SM, *et al.* (2005). Survey of potential sapstain fungi on *Pinus radiata* in New Zealand. *New Zealand Journal of Botany* **43**: 653–663.
- Traquair JA, Shaw LA, Jarvis WR (1988). *Stephanoascus farinosus*, teleomorph of *Sporothrix fungorum*. *Mycologia* **80**: 244–246.
- Travassos LR, Lloyd KO (1980). *Sporothrix schenckii* and related species of *Ceratocystis*. *Microbiological Reviews* **44**: 683–721.
- Tsang C-C, Chan JFW, Pong W-M, *et al.* (2016). Cutaneous hyalohyphomycosis due to *Parengyodontium album* gen. et comb. nov. *Medical Mycology*. <http://dx.doi.org/10.1093/mmy/myw025>.
- Upadhyay HP (1981). *A monograph of Ceratocystis and Ceratocystiopsis*. University of Georgia Press, Athens, GA, USA.
- Van der Linde JA, Six DL, De Beer ZW, *et al.* (2016). Novel ophiostomatalean fungi from galleries of *Cyrtogenius africanus* (Scolytinae) infesting dying *Euphorbia ingens*. *Antonie Van Leeuwenhoek* **109**: 589–601.
- Villarreal M, Rubio V, De Troya MT, *et al.* (2005). A new *Ophiostoma* species isolated from *Pinus pinaster* in the Iberian Peninsula. *Mycotaxon* **92**: 259–268.
- Von Arx JA (1971). Über die Typusart, zwei neue und einige weitere Arten der Gattung *Sporotrichum*. *Persoonia* **6**: 179–184.
- Weijman ACM, de Hoog GS (1985). Carbohydrate patterns and taxonomy of *Sporothrix* and *Blastobotrys*. *Antonie van Leeuwenhoek* **51**: 111–120.
- White TJ, Bruns T, Lee S, *et al.* (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols: a guide to methods and application* (Innis MA, Gelfand DH, Sninsky JJ, White TJ, eds). Academic Press, San Diego, USA: 315–322.
- Wingfield MJ, De Beer ZW, Slippers B, *et al.* (2012). One fungus, one name promotes progressive plant pathology. *Molecular Plant Pathology* **13**: 604–613.
- Zhang Y, Hagen F, Stielow B, *et al.* (2015). Phylogeography and evolutionary patterns in *Sporothrix* spanning more than 14 000 human and animal case reports. *Persoonia* **35**: 1–20.
- Zhou XD, De Beer ZW, Ahumada R, *et al.* (2004). *Ophiostoma* and *Ceratocystiopsis* spp. associated with two pine-infesting bark beetles in Chile. *Fungal Diversity* **15**: 261–274.
- Zhou XD, De Beer ZW, Wingfield MJ (2006). DNA sequence comparisons of *Ophiostoma* spp., including *Ophiostoma aurorae* sp. nov., associated with pine bark beetles in South Africa. *Studies in Mycology* **55**: 269–277.
- Zhou X, Rodrigues A, Feng P, *et al.* (2014). Global ITS diversity in the *Sporothrix schenckii* complex. *Fungal Diversity* **66**: 153–165.
- Zipfel RD, De Beer ZW, Jacobs K, *et al.* (2006). Multi-gene phylogenies define *Ceratocystiopsis* and *Grosmannia* distinct from *Ophiostoma*. *Studies in Mycology* **55**: 75–97.