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

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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 Sporothrix 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 Sporothrix 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 in- fructescences. 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. & Bullin) Z.W. de Beer, T.A. Duong & M.J. Wingf., S. aurorae (K.D. Zhou & M.J. Wingf.) 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. canthariensis (P. Romon et al.) Z.W. de Beer, T.A. Duong & M.J. Wingf., S. dentifunda (Aghayeova & 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. Romon 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 (Aghayeova & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., S. genella (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 (Aghayeova & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., S. narcissi (Limer) Z.W. de Beer, T.A. Duong & M.J. Wingf., S. nebularis (P. Romon 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. palumbinata (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. polyprotocia (Constant. & Ryman) Z.W. de Beer, T.A. Duong & M.J. Wingf., S. proliferata (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.

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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, 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 & Guogeret 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 (Van 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 & Marial (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 Sporothrix. The previous
year, Hedgcoc (1906) described the synasexual morphs of some Graphium spp. also as Sporotrichum. Apart from Sporotrichum, both Hedgcoc (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-Kääriä 1953, Hunt 1956). Some authors applied other generic names to describe asexual morphs of Ophiostoma, such as Cylindrocarpium, Hormodendron (Robak 1932), Hyalodendron (Goidanich 1935, Georgescu et al. 1948), and Rhizoclinium (Georgescu et al. 1948, Szerbin-Parfenenik 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 Sporothrix 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 1983). 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 Ophiostomatatales. Hausner et al. (2000) produced a SSU phylogeny that included seven species in the Ophiostomatatales. 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, Kamga Nkuekam et al. 2012). This was also evident in the most comprehensive phylogenies of the Ophiostomatatales 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 synnematous, pestalotum-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 Ophiostomatatales 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 Ophiostomatatales, 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 infrutescences.

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 Dolichoaascus 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 & Burns 1993) and ITS4 (White et al. 1990) were used for the ITS regions. The PCR reactions of the BT7 genes were run using primers T10 (O’Donnell & Cigelnik 1997) and Bi2b, while Bi2a and Bi2b (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’-CCGARTWCAGGAGGSCSTTC-3’) and CL3R (5’-TTCTGCATC-RAGYTGSC-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 (Katoh & 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 & Michelak 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 100th 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 Ophiostomatineae: Leptographium s. lat., Ophiostoma s. str., Fragosphaeria, Ceratocystiopsis, Raffaelea 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 Hauksworts-thiomyces (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 ‘, 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 or other | Type | Isolated from | Country | Collector | GenBank Accession numbers |
|---------------|----------|--------------|------|---------------|---------|-----------|--------------------------|
| Ceratocystis eucastansea | S. eucastansea | 1124 | 424.77 T | canker on Castanea dentata | North Carolina, USA | RW Davidson | KX590843 KX590814 KX590753 KX590781 |
| C. gossypina var. robusta | S. rossii | 1118 | 116.78 T | Dendroctonus adjunctus gallery on P. ponderosa | New Mexico, USA | RW Davidson | KX590844 KX590815 KX590754 KX590782 |
| Dolichoascus schenckii | syn. S. schenckii | 938.72 T | Human | France | F Mariat | NA | KP017094 NA AM490340 |
| O. abietinum | S. abietina | 22310 | 125.89 T | Pseudohylesinus gallery on Abies vejari | New Mexico, USA | RW Davidson | KX590845 KX590816 KX590755 KX590783 |
| O. africanum | S. africana | 823 | 125.89 T | Human | France | F Mariat | NA |
| O. albidum | syn. S. stenoceras | 1123 | 798.73 T | Pissodes pini gallery on Pinus sylvestris | Sweden | MJ Wingfield | DQ16147 DQ316199 DQ296073 NA |
| O. angusticollis | O. angusticollis | 152 | 186.86 T | Hylastes attenuatus on Pinus radiata | South Africa | XD Zhou | KX590847 DQ396796 DQ396800 KX590784 |
| O. Candida | S. candida | 26484 | 129713 T | Eucalyptus cloeziana | South Africa | G Kamgan | NA |
| O. cantabriense | S. cantabriensis | 39766 | 136529 T | Hylastes attenuates on Pinus sylvestris | South Africa | G Kamgan | NA |
| O. coronatum | O. coronatum | 37433 | 497.77 T | Ambrosia galaxy | Canada | RW Davidson | KX590851 AY924385* KX590758* KX590786* |
| O. denticulatum | O. denticulatum | 1128 | ATCC38087 T | Amygdalina garnierii | Colorado, USA | RW Davidson | KX590852 KX590816* KX590759* NA |
| O. furfuratus | O. furfuratus | 3016 | 115790 T | Quercus wood | Hungary | C Delatour | KX590853 AY495434 AY495445 KX590787 |
| O. eucalyptigena | O. eucalyptigena | 15089 | 129712 T | Eucalyptus cloeziana | South Africa | G Kamgan | NA |
| O. euskadiense | S. euskadiensis | 27318 | 122138 T | Eucalyptus pellatellus on Pinus radiata | Spain | XD Zhou | KX590854 DQ674369 EF396344 JQ438830 KX590783 |
| O. fumeum | O. fumeum | 26813 | 129712 T | Eucalyptus cloeziana | South Africa | G Kamgan | NA |
| O. fusiforme | S. fusiformis | 9968 | 112912 T | Populus nigra | Azerbaijan | D Aghayeva | DQ294354 AY280461 AY280460 JQ511967 |
| O. gemellus | S. gemella | 23057 | 121959 T | Tarsonemus sp. from Protea caffra | South Africa | F Roets | DQ821531 DQ821560 DQ821554 NA |
| O. gossypinum | S. gossypina | 22311 | ATCC18999 T | P. ponderosa | New Mexico, USA | RW Davidson | KX590855 KX590819 KX590761 KX590789 |
| O. grande | O. grande | 22307 | 350.78 T | Diatypus fruticuloides on bark | Brazil | RD Dumont | KX590857 NA NA |
| O. grandicarpum | O. grandicarpum | 1600 | 250.88 T | Quercus robur | Poland | T Kowalski | KX590858 KX590820* KX590762* NA |
| O. lunatum | S. lunata | 10563 | 112927 T | Carpinus betulus | Austria | T Kursits | KX590859 AY280485 AY280461 JQ511967 |
| O. macrosorum | O. macrosorum | 14176 | 367.53 T | Ips amplus | Sweden | H Francke-Grosman | EU177488 AY280485 AY280461 JQ511967 |
| O. microsporum | O. microsporum | 01712 | 440.69 NT | Quercus sp. | Virginia, USA | EG Kuhlman | KX590860 KX590822* KX590764* NA |
| O. narcissi | S. narcissi | 22311 | 138.50 T | Narcissus sp. | Netherlands | DP Limber | KX590861 AY194510 KX590765 KX590791 |
| O. nebulare | S. nebularis | 22797 | 138.50 T | Orthotopicus erosa on Pinus radiata | Spain | P Romon | KX590862 KX590823 NA JQ438829 |
| O. nigricarpum | O. nigricarpum | 651 | 638.66 P | Pseudotsuga menziesii | Idaho, USA | RW Davidson | KX590863 KX590824 KX590766 JQ438828 |

**Notes:**
- Bold type indicates Genbank numbers for sequences obtained in the present study.
- CMW: Culture collection number.
- Type: Isolated from.
Table 1. (Continued)

| Previous name | New name | CMW\(^1\) or other | Type | Isolated from | Country | Collector | GenBank Accession numbers |
|---------------|----------|---------------------|------|---------------|---------|-----------|--------------------------|
| O. nigricarpum | O. nigricarpum | 650 637.66 | T | Abies sp. | Idaho, USA | RW Davidson | NA |AY280489* AY280479* NA |
| O. nigrogranum | S. nigrograna | 14487 MAFF410943 | T | Pinus densiflora | Japan | H Masuya | KX590863 KX590825 NAKX590864 KX590866 KX590864 KU639631 KU639628 | KX590792 |
| O. noisomeae | O. noisomeae | 40326 141065 | T | Rana peraeola melanophloeo | South Africa | T Musuvgw | NA | KX590865 KX590826 KX590767 KX590793 |
| O. noisomeae | O. noisomeae | 40329 141066 | P | Rana peraeola melanophloeo | South Africa | T Musuvgw | NA | KX590865 KX590826 KX590767 KX590793 |
| O. ponderosae | O. ponderosae | 37953 ATCC26665 | T | P. ponderosa | Arizona, USA | TE Hinds | NA | KX590866 KX590870 KX590767 KX590796 |
| O. ponderosae | 'O. ponderosae 2' | 128 RWD899 | Not known | USA | TE Hinds | NA | KX590866 KX590870 KX590767 KX590796 |
| O. proleferum | S. prolefera | 37435 251.88 | T | Quercus robur | Poland | T Kowalski | NA | KX590869 KX590829 KX590770 KX590797 |
| O. protea | S. protea | 1107 116654 | T | P. caffra | South Africa | MJ Wingfield | NA | KX590815 KX316201 KX316163 KX590816 |
| O. protea-sedis | S. protea-sedis | 28601 124910 | T | P. caffra | South Africa | MJ Wingfield | NA | KX590815 KX316201 KX316163 KX590816 |
| O. rostrocoronatum | O. rostrocoronatum | 456 434.77 | T | P. caffra | South Africa | MJ Wingfield | NA | KX590815 KX316201 KX316163 KX590816 |
| O. splendens | S. splendens | 897 116379 | T | P. caffra | South Africa | MJ Wingfield | NA | KX590815 KX316201 KX316163 KX590816 |
| O. stenoceras | S. stenoceras | 3202 237.32 | T | P. caffra | South Africa | MJ Wingfield | NA | KX590815 KX316201 KX316163 KX590816 |
| O. tenellum | S. tenellum | 37439 188.86 | T | P. caffra | South Africa | MJ Wingfield | NA | KX590815 KX316201 KX316163 KX590816 |
| O. thermarum | S. thermara | 38930 139747 | T | P. caffra | South Africa | MJ Wingfield | NA | KX590815 KX316201 KX316163 KX590816 |
| O. valdivianum | O. valdivianum | 449 484.83 | T | P. caffra | South Africa | MJ Wingfield | NA | KX590815 KX316201 KX316163 KX590816 |
| O. zambiensis | S. zambiensis | 28604 124912 | T | P. caffra | South Africa | MJ Wingfield | NA | KX590815 KX316201 KX316163 KX590816 |

* Continued on next page */
| Previous name | New name | CMW \(^1\) or other | Type | Isolated from | Country | Collector | LSU Accession numbers | ITS Accession numbers | BT Accession numbers | CAL Accession numbers |
|---------------|----------|----------------------|------|---------------|---------|-----------|----------------------|----------------------|----------------------|----------------------|
| S. curviconia | ‘S. curviconia 2’ | 17163 541.84 | T | Pinus radiata log | Chile | HL Peredo | KX590881 | KX590836 | KX590777 | JQ511968 |
| S. dimorphospora | S. dimorphospora | 12529 553.74 | T | Soil | Canada | RAA Morall | NA | AY495428 | AY495439 | NA |
| | | 37446 125442 | T | Soil | Spain | C Silvera | KX590882 | FJ549661 | FJ547379 | KX590806 |
| S. fungorum | Uncertain | 17165 259.70 | T | Fomes fomentarius basidiome | Germany | W Gams | KX590883* | KX590837* | NA | NA |
| S. globosa | S. globosa | 29128 120340 | T | Human face | Spain | C Rubio | KX590884 | KX590838 | AM116966 | AM166908 |
| S. guttuliformis | S. guttuliformis | 17167 437.76 | T | Soil | Malaysia | T Furukawa | KX590885 | KX590839 | KX590778 | KX590807 |
| S. humicola | S. humicola | 7618 118129 | T | Soil | South Africa | HF Vismer | EF139114 | AF454472 | EF139100 | KX590808 |
| S. inflata | ‘S. inflata 2’ | 12526 156.72 | T | Greenhouse soil | Netherlands | H Kaastra-Howeler | NA | AY495425 | AY495436 | NA |
| S. inflata | S. inflata | 12527 239.86 | T | Wheat field soil | Germany | W Gams | DQ294351 | AY495426 | AY495437 | NA |
| S. itsvo | S. itsvo | 40370 141063 | T | Rapanea melanophloeos | South Africa | T Musvuugwa | NA | KX590840 | KU639625 | NA |
| S. lignivora | Hawksworthiozymes lignivora | 18600 119148 | T | Eucalyptus utility poles | South Africa | EM de Meyer | EF139119 | EF127890* | EF139104* | NA |
| S. luniei | S. luniei | 18599 119147 | T | Eucalyptus utility poles | South Africa | EM de Meyer | KX396545 | EF127889* | EF139103* | NA |
| S. mexicana | S. mexicana | 17210 937.72 | T | Human skin | South Africa | H Lurie | KX590886 | AB128012 | AM747289 | AM747302 |
| S. nivea | syn. S. pallida | 17168 150.87 | T | Sediment in water purification plant | Germany | G Teuscher, F Schauer | KX590888 | EF127879 | KX590779 | KX590809 |
| S. nothofagi | S. nothofagi | 37658 NZFS519 | T | Nothofagus fusca | New Zealand | W Faulds | KX590889 | NA | KX590780* | KX590810* |
| S. pallida | S. pallida | 17209 131.56 | T | Stemonitis fusca | Japan | K Tubaki | EF139121 | EF127880 | EF139110 | KX590811 |
| S. rapaneae | S. rapaneae | 40369 141060 | T | Rapeanella melanophloeos | South Africa | T Musvuugwa | NA | KU595583 | KU639624 | KU639609 |
| S. schenckii | S. schenckii | 28351 359.36 | T | Human | USA | CF Perkins | KX590890 | KX590842 | AM116911 | AM117437 |
| S. stylites | S. stylites | 14543 118848 | T | Pine utility poles | South Africa | EM de Meyer | EF139115 | EF127883 | EF139096 | KX590812 |
| S. variecibatus | S. variecibatus | 23051 121961 | T | Trichourpoda sp. from Protea repens | South Africa | F Roets | DQ821537 | DQ821568 | DQ821539 | KX590813 |

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.

\(^1\) CMW = Culture Collection of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa.

\(^2\) 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 Fragosphearia, Ceratocystis 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 recognised 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 Ceratocystis and Lineage C were used as outgroups in the BT data set because no BT sequences were available for Fragosphearia. Apart from species complex 1, all four of 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 (+/−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 (3I/−5). The only exception was O. nothofagi that contained intron 4, but lacked intron 5 (3I/4−). The fragment of the latter species was too short to reflect differences in BT sequences between closely related taxa.

The analyses of the CAL gene region (Fig. 4), only Lineage C was included as outgroup because CAL sequences were not available for Fragosphearia and Ceratocystis. 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 3I4−, with the only exceptions found in O. nothofagi and S. bruneoviolacea (in Group I), which had all three introns (3I4/5). 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. Ascii 8-spored, evanescent, globose to broadly clavate. Ascospores hyaline, aseptate, lunate, allantoid, reniform, orange section-shaped, sheath absent. Asexual states micromenomatous, 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 synonyms 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 Grosmaniella penicillata complex (De Beer & Wingfield 2013, De Beer et al. 2013).
2. Sporothrix aemulophila T. Musvuugwa et al., Antonie van Leeuwenhoek 108: 945. 2015. Note: Forms part of the S. candida complex (Figs 2–4).

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

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.

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.
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.

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.

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

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

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.

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.

*Note*: 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.

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 (B) 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.
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 |
|-------|---------|--------------|---------|--------|--------------|------|-------------|------------|-------------|-----------|
| **SPOROTHER** | *S. brasiliensis* | n | h, p | br | p | 3/4/5 | 3/4/- | South America |
| **Group A** | *S. globosa* | n | h, p | br | p, s | hay | 3/4/5 | 3/4/- | Asia, Europe, North America, South America |
| **Group B** | *S. lutea* | n | h | w | p | 3/4/5 | 3/4/- | Africa |
| **Group C** | *S. schenckii* | n | h, p | br | p, s | h, hay | 3/4/5 | 3/4/- | Africa, Asia, Australasia, Europe, Central-, North- & South America |
| **Group D** | *S. candida* | y | h | w | h | 3/4/- | Africa |
| **Group E** | *S. ravenelii* | y | h | w | h | 3/4/- | Africa |
| **Group F** | *S. capsulata* | y | h | w | s? | c | 3/4/- | Africa, Asia, Australasia, Europe, North America |
| **Group G** | *S. auroralis* | y | h | w | h | 3/4/- | Africa |
| **Group H** | *S. anchusa* | y | h | w | s | h,c | 3/4/- | Africa |
| **Group I** | *S. inflata* | y | h | w | p | m | 3/4/- | Africa |
| **Group J** | *S. pallida* | n | h | s | h | 3/4/- | Africa |
| **Group K** | *S. dimorphospora* | n | h | p | g | s | 3/4/- | Europe |
| **Group L** | *S. dimorphotheca* | n | h | w | p | s | 3/4/- | South America |
| **Group M** | *S. globosa* | n | h | w | p | s | 3/4/- | Africa |
| **Group N** | *S. globosa* | n | h | w | p | s | 3/4/- | Africa |
| **Group O** | *S. globosa* | n | h | w | p | s | 3/4/- | Africa |
| **Group P** | *S. globosa* | n | h | w | p | s | 3/4/- | Africa |
| **Group Q** | *S. globosa* | n | h | w | p | s | 3/4/- | Africa |
| **Group R** | *S. globosa* | n | h | w | p | s | 3/4/- | Africa |
| **Group S** | *S. globosa* | n | h | w | p | s | 3/4/- | Africa |
| **Group T** | *S. globosa* | n | h | w | p | s | 3/4/- | Africa |
| **Group U** | *S. globosa* | n | h | w | p | s | 3/4/- | Africa |
| **Group V** | *S. globosa* | n | h | w | p | s | 3/4/- | Africa |
| **Group W** | *S. globosa* | n | h | w | p | s | 3/4/- | Africa |

**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 infructescens, h = hardwood, f = macrofungus fruiting body; **Beetle/mite:** bb = bark beetle, ab = ambrosia beetle, c = cerambycid, m = mite.
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: Hurnicola 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. plurianulatum 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 epithel 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 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 epigloea]
Synonym: Ophiostoma epigloea (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. (1983) 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. aurora 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 (Kamgang et al.) Z.W. de Beer, T.A. Duong & M.J. Wingf., comb. nov. MycoBank MB817573.
Basionym: Ophiostoma fumeum Kamgang 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 7Tsequence 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 perithecium morphology. 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. abietinum. 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 Vege 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: Ceratoctis narcissi (Limber) J. Hunt, Llydia 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 nebulae 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 hyalorhinocadiella-like asexual morph and sheathed ascospores. However, our sequences of the ex-type isolate confirms its placement close to S. nebularia in Group G of Sporothrix (Figs 1 and 2).

35. Sporothrix pallida (Tubaki) Matush., Icon. microfung. Matush. 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 prolifer**a (Kowalski & Butin) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov**. MycoBank MB817584. **Basionym**: Ceratocystis prolifer 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 rapaneae** 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 (Upadhay 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, B7 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. **Synonym**: Sporotrichum beurmannii Matr. & Ramond, Compt. Rend. Hebd. Séances Mém. Soc. Biol. 2: 380. 1905. **Sporotrichosis 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: Sporotrichosis, 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 Sporotrichosis, 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 (Endomyctetaeae) 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 (Staffel 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 Skogsför. Tidskr. 32: 408. 1934.

**Ceratocystis stenoceras** (Robak) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.

**Ophiostoma albium** Math.-Käärik, Medd. Skogsforskninginst. 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 albium* 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. albium* 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. albium* is a synonym of *S. stenoceras*.

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

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

48. **Sporothrix thermarum** (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.* MycoBank 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 ASEXUAL 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 macrosorum** (Francke-Gros.) Z.W. de Beer & M.J. Wingf. In Seifert et al., The Ophiostomatoid Fungi: 256. 2013.

**Basionym:** Trichosporum tingens var. macrosorum Francke-Gros., Medd. Skogsforskninginst. 41: 24. 1952 [as ‘Trichosporum tingens var. macrosorum’]

**Synonyms:** Ambrosiella macrosora (Francke-Gros.) L.R. Batra, Mycologia 59: 980. 1967.
Hyalorhinocladiella macrospora (Francke-Grosen.) 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. pluriannullatum 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, Hawksworthomyces (Fig. 1) (De Beer et al. 2016). The current name species name is Hawksworthomyces lignivora (de Mey. et al.) Z.W. de Beer et al. (De Beer et al. 2016).

6. Sporothrix pinira (Goid.) Morelet, Ann. Sci. Nat. Arch. Toulon et du Var 44: 110. 1992. [as ‘pinirum’] Basionym: Hyalodendron pinirum 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. (Grobbelet et al. 2009, De Beer et al. 2013).

7. Sporothrix roboris (Georgescu & Teodoru) Grobbelaar 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 (Grobbelet 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 subannulatum 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 ASEXUAL 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. rostrocoronatum 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. brunniovioleacea, 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 noncateenate and cateenate 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. Asexual and asexual morphology morph morphology suggests 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 nigrocarpa]
   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 Musvugwa et al., Antonie van Leeuwenhoek 109: 887. 2016.

Notes: Musvugwa 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.
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 Ochowevski & Reid (1974), but suggested to be a synonym of *O. tenellum* by Upadhyay (1981) and listed as such by Villareal 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 valdivianum Butin. In Butin & Aguilar, 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 & Aguilar 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 isolate places this species with other *Sporothrix* species, 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 asexual 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 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. **Sphaeronomex epiglaeum** Berk. & M.A. Curtis, Grevillea 2: 84. 1873.

Notes: *Sphaeronomex epiglaeum* from *Tremella* fruiting bodies in the USA was considered a synonym of *O. epiglaeum* from the same host in Argentina according to Guerrero (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 Berkely, 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 chordracis** B. Huang, M.Z. Fan & Z.Z. Li, Mycosystems 16: 88. 1997.

Notes: Although the origin of this species from a cotton grass-hopper 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. infiata* 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 insitiatiramosa** 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 hellenii** 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. hellenii* might belong with the cordycipitalean *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). Weijsman & 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*: Weijsman & 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 Weijsman & 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 ‘tarda-lutea’], 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 septe 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 cifernii, currently treated as a synonym of Trichomonausc ciferrii (Trichomonauscaceae, Saccharomyzetales) (Kurtzman & Robnett 2007). This confirms the synonymy of S. catenata with St. cifernii 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 (Microstomatales, 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 (Microstomatales, 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 Trichomonausc 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 Blastobotrux 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 Trichomonausc as defined by Kurtzman & Robnett (2007). However, further phylogenetic analyses including sequences of more gene regions and species belonging to the Trichomonauscaceae (Saccharomyzetales) (Kurtzman & Sugiyama 2015) should be done to confirm the generic placement of S. fungorum before any 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 Dacrymyxetales (Moore 1987, Middelhoven et al. 2000).

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

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

Note: Currently treated as Quambalaria piteureka (Microstomatales, Ustilaginomycetes) (De Beer et al. 2006).

9. Sporothrix pusilla U. Braun & Crous. In Braun, Monogr. Cercosporella, Ramularia Allied Genera 2: 416. 1998.

Note: A basidiomycete now treated as Quambalaria pusilla (Microstomatales, 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 tuberum*.

**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 on asexual fungi (*de Hoog 1974*) has been redefined in line with the one fungus 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. nothofagii* (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. plurianullatum* 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*), *Ceratocystis* (*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-infecting bark beetles. Some smaller lineages are exceptions in this regard: the *O. ulmi* complex in *Ophiostoma* s. str. and *Fragsphaeria* 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-infecting bark beetles. Interestingly, five of these, *S. abietina*, *S. aurorae*, *S. cantabriensis*, *S. euskadiensis*, and *S. nebularis* are associated specifically with root-infecting 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, Ochoweccki & 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 Clad* (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 (*Ajielo & 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-Martínez 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* (*Morete 1995, Bommer et al. 2009*).
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 confiers 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. auroae 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 (Mcsuuwaga 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 anthropods. 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 & Srůtka 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 with not enough statistical support to define it as 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 (Mantí 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. guttilliformis. 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. rapaneae and S. itso from inner bark of Rapanea trees (Mcsuuwaga 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 Ernsti 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 were separated into 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. pinna, S. robberis 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. ligniora, has recently been described in the new genus, Hawksworthiomycetes (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. ponderaeae. Many of these species in other genera in the Ophiostomatales that produce sporothrix-like asexual morphs, also produce hyalorhinocladiella- or synnema-tous pesotum-like synasexual morphs.

Sporothrix fulorum 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 Tri-chomosorus and Blastobotrys (Saccharomycetales, Saccharomyces), 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 synonyms 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.

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