

# Generic boundaries in the *Ophiostomatales* reconsidered and revised

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**Abstract:** The *Ophiostomatales* was erected in 1980. Since that time, several of the genera have been redefined and others have been described. There are currently 14 accepted genera in the Order. They include species that are the causal agents of plant and human diseases and common associates of insects such as bark beetles. Well known examples include the Dutch elm disease fungi and the causal agents of sporotrichosis in humans and animals. The taxonomy of the *Ophiostomatales* was confused for many years, mainly due to the convergent evolution of morphological characters used to delimit unrelated fungal taxa. The emergence of DNA-based methods has resolved much of this confusion. However, the delineation of some genera and the placement of various species and smaller lineages remains inconclusive. In this study we reconsidered the generic boundaries within the *Ophiostomatales*. A phylogenomic framework constructed from genome-wide sequence data for 31 species representing the major genera in the Order was used as a guide to delineate genera. This framework also informed our choice of the best markers from the currently most commonly used gene regions for taxonomic studies of these fungi. DNA was amplified and sequenced for more than 200 species, representing all lineages in the Order. We constructed phylogenetic trees based on the different gene regions and assembled a concatenated data set utilising a suite of phylogenetic analyses. The results supported and confirmed the delineation of nine of the 14 currently accepted genera, *i.e.* *Aureovirgo*, *Ceratocystiopsis*, *Esteya*, *Fragosphaeria*, *Graphilbum*, *Hawksworthiomyces*, *Ophiostoma*, *Raffaelea* and *Sporothrix*. The two most recently described genera, *Chrysosphaeria* and *Intubia*, were not included in the multi-locus analyses. This was due to their high sequence divergence, which was shown to result in ambiguous taxonomic placement, even though the results of phylogenomic analysis supported their inclusion in the *Ophiostomatales*. In addition to the currently accepted genera in the *Ophiostomatales*, well-supported lineages emerged that were distinct from those genera. These are described as novel genera. Two lineages included the type species of *Grosmannia* and *Dryadomyces* and these genera are thus reinstated and their circumscriptions redefined. The descriptions of all genera in the *Ophiostomatales* were standardised and refined where this was required and 39 new combinations have been provided for species in the newly emerging genera and one new combination has been provided for *Sporothrix*. The placement of *Afroraffaelea* could not be confirmed using the available data and the genus has been treated as *incertae sedis* in the *Ophiostomatales*. *Paleoambrosia* was not included in this study, due to the absence of living material available for this monotypic fossil genus. Overall, this study has provided the most comprehensive and robust phylogenies currently possible for the *Ophiostomatales*. It has also clarified several unresolved One Fungus-One Name nomenclatural issues relevant to the Order.

**Key words:** Generic boundaries, new taxa, nomenclature, *Ophiostomataceae*, *Ophiostomatales*, *Sordariomycetidae*, taxonomy.

**Taxonomic novelties: New genera:** *Harringtonia* Z.W. de Beer & M. Procter, *Heinzbutinia* Z.W. de Beer & M. Procter, *Jamesreidia* Z.W. de Beer & M. Procter, *Masuyamyces* Z.W. de Beer & M. Procter. **New species:** *Masuyamyces massoniana* M. Procter & Z.W. de Beer. **New combinations:** *Dryadomyces montetyi* (M. Morelet) M. Procter & Z.W. de Beer, *Dryadomyces quercivorus* (Kubono & Shin. Ito) M. Procter & Z.W. de Beer, *Dryadomyces quercus-mongolicae* (K.H. Kim *et al.*) M. Procter & Z.W. de Beer, *Dryadomyces sulphureus* (L.R. Batra) M. Procter & Z.W. de Beer, *Graphilbum pusillum* (Masuya) M. Procter & Z.W. de Beer, *Grosmannia abieticolens* (K. Jacobs & M.J. Wingf.) M. Procter & Z.W. de Beer, *Grosmannia altior* (Paciura *et al.*) M. Procter & Z.W. de Beer, *Grosmannia betulae* (Jankowiak *et al.*) M. Procter & Z.W. de Beer, *Grosmannia curviconidia* (Paciura *et al.*) M. Procter & Z.W. de Beer, *Grosmannia euphyes* (K. Jacobs & M.J. Wingf.) M. Procter & Z.W. de Beer, *Grosmannia fenglinhensis* (R. Chang *et al.*) M. Procter & Z.W. de Beer, *Grosmannia gestamen* (de Errasti & Z.W. de Beer) M. Procter & Z.W. de Beer, *Grosmannia innermongolica* (X.W. Liu *et al.*) M. Procter & Z.W. de Beer, *Grosmannia pistaciae* (Paciura *et al.*) M. Procter & Z.W. de Beer, *Grosmannia pruni* (Masuya & M.J. Wingf.) M. Procter & Z.W. de Beer, *Grosmannia taigensis* (Linnak. *et al.*) M. Procter & Z.W. de Beer, *Grosmannia trypodendri* (Jankowiak *et al.*) M. Procter & Z.W. de Beer, *Harringtonia aguacate* (D.R. Simmons *et al.*) M. Procter & Z.W. de Beer, *Harringtonia brunnea* (L.R. Batra) M. Procter & Z.W. de Beer, *Harringtonia lauricola* (T.C. Harr. *et al.*) Z.W. de Beer & M. Procter, *Heinzbutinia grandicarpa* (Kowalski & Butin) Z.W. de Beer & M. Procter, *Heinzbutinia microspora* (Arx) M. Procter & Z.W. de Beer, *Heinzbutinia solheimii* (B. Strzalka & Jankowiak) Z.W. de Beer & M. Procter, *Jamesreidia coronata* (Olchow. & J. Reid) M. Procter & Z.W. de Beer, *Jamesreidia nigricarpa* (R.W. Davidson) M. Procter & Z.W. de Beer, *Jamesreidia rostrocoronata* (R.W. Davidson & Eslyn) M. Procter & Z.W. de Beer, *Jamesreidia tenella* (R.W. Davidson) Z.W. de Beer & M. Procter, *Leptographium cainii* (Olchow. & J. Reid) M. Procter & Z.W. de Beer, *Leptographium europioides* (E.F. Wright & Cain) M. Procter & Z.W. de Beer, *Leptographium galeiforme* (B.K. Bakshi) M. Procter & Z.W. de Beer, *Leptographium pseudoeuropioides* (Olchow. & J. Reid) M. Procter & Z.W. de Beer, *Leptographium radiaticola* (J.J. Kim *et al.*) M. Procter & Z.W. de Beer, *Masuyamyces acarorum* (R. Chang & Z.W. de Beer) M. Procter & Z.W. de Beer, *Masuyamyces ambrosius* (B.K. Bakshi) M. Procter & Z.W. de Beer, *Masuyamyces botuliformis* (Masuya) Z.W. de Beer & M. Procter, *Masuyamyces jilinensis* (R. Chang *et al.*) M. Procter & Z.W. de Beer, *Masuyamyces lotiformis* (Z. Wang & Q. Lu) M. Procter & Z.W. de Beer, *Masuyamyces pallidulus* (Linnak. *et al.*) M. Procter & Z.W. de Beer, *Masuyamyces saponiodorus* (Linnak. *et al.*) M. Procter & Z.W. de Beer, *Sporothrix longicollis* (Masseo & E.S. Salmon) M. Procter & Z.W. de Beer.

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## INTRODUCTION

The *Ophiostomatales* (*Sordariomycetidae*, *Ascomycota*), was described by Benny & Kimbrough (1980) accommodating the single family *Ophiostomataceae*. The Order includes species that are the causal agents of plant and human diseases as well as common associates of wood infesting insects such as bark beetles (Wingfield *et al.* 1993, Seifert *et al.* 2013). Well known examples are the Dutch elm disease fungi and the causal agents of sporotrichosis in humans and animals (Figs 1, 2). As described, this Order originally accommodated four genera, *Ophiostoma*, *Ceratocystiopsis*, *Sphaeronaemella* and *Ceratocystis*. These authors considered *Ceratocystis* distinct from *Ophiostoma* based on cell wall constituents and conidiogenesis (Weijman & De Hoog 1975, Seifert *et al.* 2013). Upadhyay (1981) treated *Ophiostoma* as a synonym of *Ceratocystis* based on morphological similarities such as their long-necked ascocarps that produce sheathed ascospores in sticky droplets to facilitate arthropod dispersal (Upadhyay 1981, Malloch & Blackwell 1993). In the 1990's, DNA sequence data confirmed that *Ophiostoma* and *Ceratocystis* resided in two distinct Orders of the fungi (Hausner *et al.* 1993c, Spatafora & Blackwell 1994). *Ceratocystis* has subsequently been shown to represent several morphologically and ecologically distinct genera in the *Ceratocystidaceae* (*Microascales*) (De Beer *et al.* 2013a, 2014, Nel *et al.* 2018, Mayers *et al.* 2015, 2020).

The *Ophiostomatales* as it is currently defined accommodates a single family, the *Ophiostomataceae* (De Beer *et al.* 2013a), which was initially described in 1932 (Nannfeldt 1932). At the time, it included *Ophiostoma*, with *Endoconidiophora* and *Ceratocystis* as synonyms (Melin & Nannfeldt 1934). The family was treated in various Orders prior to 1980 (De Beer *et al.* 2013a). Apparently unaware of Benny & Kimbrough's (1980) study, Upadhyay (1981) re-defined the *Ophiostomataceae* with *Ceratocystis* as type genus, and *Ophiostoma*, *Sphaeronaemella*, *Grosmannia* and *Europhium* as synonyms, and with *Ceratocystiopsis* as a distinct new genus. However, the DNA-based distinction between *Ceratocystis* and *Ophiostoma* led to their inevitable separation and emended definitions of the *Ceratocystidaceae* and *Ophiostomataceae* (Wingfield *et al.* 1993, Réblová *et al.* 2011, De Beer *et al.* 2013a, 2016a).

The first attempt to resolve generic boundaries within the *Ophiostomatales* subsequent to its separation from the *Ceratocystidaceae* was made by Zipfel *et al.* (2006). Based on phylogenies constructed from ribosomal DNA and  $\beta$ -tubulin sequences and including 55 taxa, they recognised *Ophiostoma*, *Ceratocystiopsis* and *Grosmannia* as distinct sexual genera. Following the dual nomenclature system at the time, asexual *Sporothrix* and *Leptographium* species retained their names in these genera, although they respectively grouped in *Ophiostoma* and *Grosmannia*.

After 20 years of DNA-based taxonomy and in the wake of the abandonment of a dual nomenclature for the fungi (Hawksworth *et al.* 2011, Hawksworth 2012), De Beer & Wingfield (2013) revised the *Ophiostomatales*, considering all published ribosomal large subunit (LSU) and internal transcribed spacer (ITS) sequences, including 266 species. They redefined *Ophiostoma sensu stricto*, *Raffaelea s.s.*, *Ceratocystiopsis*, *Fragosphaeria* and *Graphilbum*, and recognised 18 species complexes within the various genera of the *Ophiostomatales*. However, they concluded that the rDNA-based phylogenies were not sufficiently robust to resolve the generic status of the *Sporothrix schenckii*-*Ophiostoma stenoceras* species complex, or that of various lineages within what they defined as *Leptographium sensu lato*. Their phylogenies also suggested that

ambrosial species previously treated as *Raffaelea* did not form a monophyletic group.

After the revision of the *Ophiostomatales* by De Beer & Wingfield (2013), the majority of studies focused on new species descriptions (Romón *et al.* 2014a, b, Musvuugwa *et al.* 2015, 2016, De Errasti *et al.* 2016, Simmons *et al.* 2016, Chang *et al.* 2017, Marincowitz *et al.* 2017, 2020, *etc.*) and on resolving issues within species complexes (Ando *et al.* 2016, Linnakoski *et al.* 2016, Jankowiak *et al.* 2017, Yin *et al.* 2019, 2020, *etc.*).

De Beer *et al.* (2016a) reconsidered the status of the *S. schenckii*-*O. stenoceras* complex, providing sequences for four gene regions of 65 species with sporothrix-like asexual morphs. They concluded that *Sporothrix* represented a distinct genus including 51 species and incorporated the characters of the sexual morphs of many of the species, previously treated as *Ophiostoma*, in the emended definition of *Sporothrix*. A lineage including some of the remaining sporothrix-like species that did not form part of the newly defined genus were provided with the new genus name, *Hawksworthiomyces*, in a subsequent paper (De Beer *et al.* 2016b). In addition, Van der Linde *et al.* (2016) and Bateman *et al.* (2017) described *Aureovirgo* and *Afroraffaelea* respectively as novel, monotypic genera in the Order. In 2018, a fungus was discovered preserved in amber alongside an ambrosia beetle, leading to the description of *Paleoambrosia*. The genus was treated in the *Ophiostomatales* based on morphological characters resembling *Raffaelea* species (Poinar & Vega 2018). Most recently, Nel *et al.* (2021) described two new genera, *Chrysosphaeria* and *Intubia*, from the abandoned combs of fungus-growing termites (*Termitomyces*) in South Africa.

In this study, we reconsidered and redefined the unresolved boundaries of genera including *Leptographium*, *Raffaelea* and some smaller lineages in the *Ophiostomatales*. To achieve this goal, we selected four gene regions based on a phylogenomic framework constructed from genome-wide sequence data for representative ophiostomatalean species. Sequence data for these four gene regions were then generated for as many species in the Order as possible, and phylogenetic analyses were conducted.

## MATERIALS AND METHODS

### Fungal isolates and DNA extraction

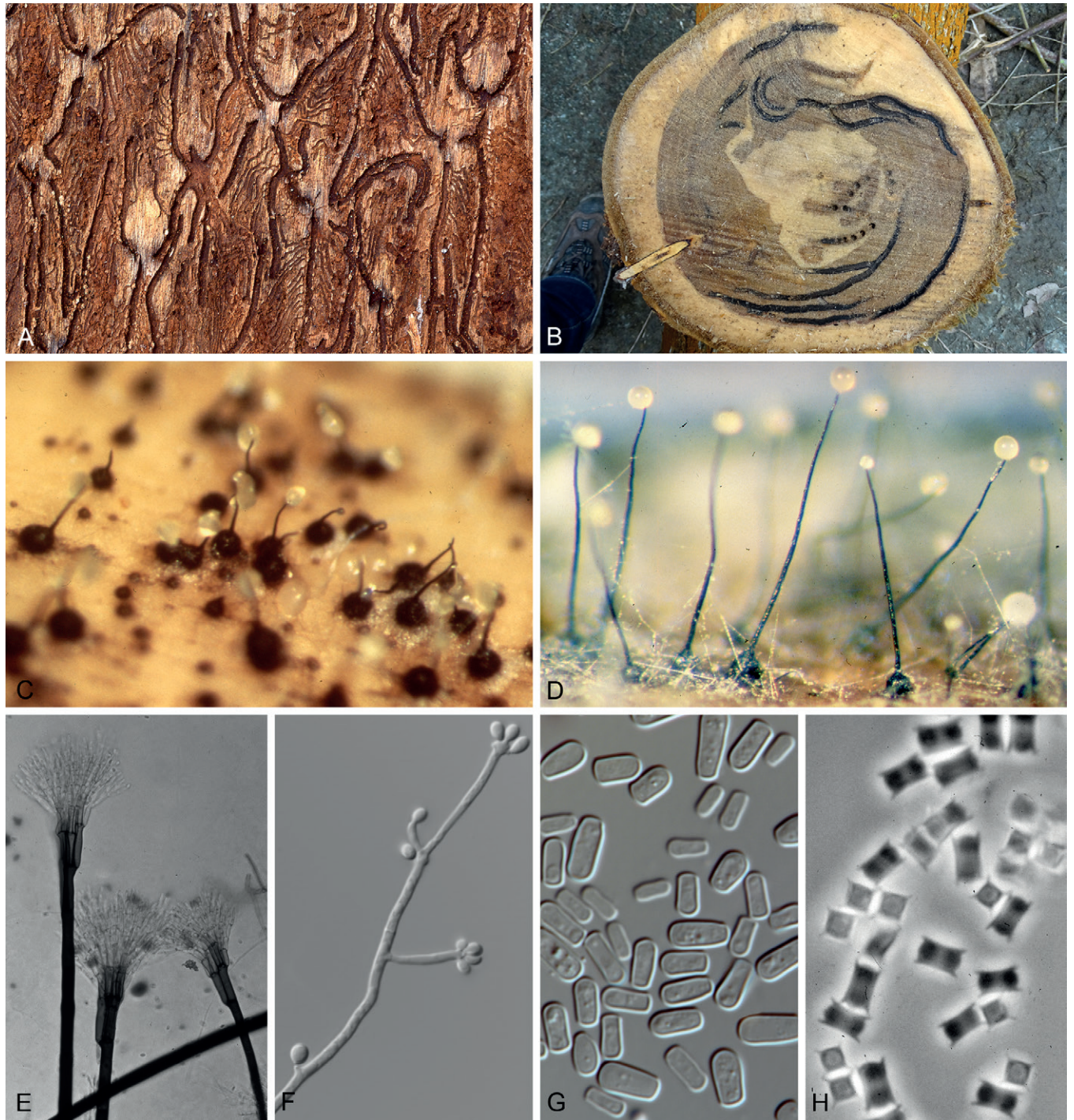
Fungal cultures used in this study were obtained from the Culture Collection (CMW) of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa, and the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, the Netherlands. Isolates were grown on 2 % malt extract agar (MEA: 20 g malt extract, 20 g agar, 1 L dH<sub>2</sub>O) at room temperature; initially with streptomycin (0.4 g/L, Sigma-Aldrich, Kempton Park, South Africa) and cycloheximide (0.5 g/L, Sigma-Aldrich, Kempton Park, South Africa) supplemented in the media, then sub-cultured to MEA, and maintained at 4 °C after optimal growth had occurred. DNA was extracted following the protocol described by Duong *et al.* (2012).

### Phylogenomic analyses

Available genome sequences for 31 species representing 11 of 14 currently recognised genera (excluding *Afroraffaelea*, *Aureovirgo* and *Paleoambrosia*) in the *Ophiostomatales* (Supplementary



**Fig. 1.** Ecological niches in which genera and species residing in the *Ophiostomatales* are found. **A.** *Ulmus americana* street trees dying as a result of Dutch Elm Disease (photo: D.W. French). **B.** Symptoms of infection by the human pathogen *Sporothrix schenckii* (photo: Prof. Dr Flávio de Queiroz Telles Filho, Federal University of Paraná, Brazil). **C.** Signage in Yellowstone National Park emphasising the important role that bark beetles (and by extension their fungal symbionts) play in the ecology of conifer ecosystems. **D.** Blue stain in conifer timber caused by numerous species of Ophiostomatoid fungi. **E.** *Hylobius rhizophagus* (root collar weevil) squashed onto the surface of agar medium containing cycloheximide selective for many genera and species of *Ophiostomatales* and in this case *Leptographium procerum*. **F.** Infertencesences of a *Protea* species in which numerous species of Ophiostomatoid fungi can be found. **G.** Douglas fir (*Pseudotsuga menziesii*) trees dying as a result of black stain root disease caused by *Leptographium wageneri* var. *pseudotsugae* (Photo: F.W. Cobb). **H.** *Pinus resinosa* trees dying as a result of mass infestation by *Ips pini* and associated *Ophiostoma minus*.



**Fig. 2.** Ecological niches of Ophiostomatoid fungi and micrographs providing examples of structures typical of these fungi. **A.** Transverse stellate gallery systems of *Ips schmutzenhoferi* in the bark of a *Pinus spinulosa* tree, showing blue-stain around nuptial chambers and female galleries. **B.** Section through a *Eucalyptus* stem infested by the ambrosia beetle *Megaplatypus mutatus* showing tunnels in which species of *Ophiostomatales* occur. **C, D.** Ascomata of *Ophiostoma ulmi* (**C**) (photo: D.W. French) and *O. pilliferum* (**D**) (photo: Z.W. de Beer) with sticky ascospore masses at their apices, illustrating the manner by which these fungi easily attach to the insects that carry them. **E.** Conidiophores of *Leptographium procerum*, illustrating asexual structures well suited to being vectored by insects. **F.** Conidigenous cells of a *Sporothrix* sp. **G.** Typical single-celled conidia found in most species of *Ophiostomatales*. **H.** Many species of *Ophiostomatales* have ascospores with sheaths such as these pillow-shaped spores in *Ophiostoma ips*.

Table S1) were used to construct a phylogenomic tree. Two species of *Diaporthales* (*Cryphonectria parasitica* and *Diaporthe ampelina*), two species of *Magnaporthales* (*Magnaporthe grisea* and *Magnaporthe poae*), and one species of *Togniniales* (*Phaeoacremonium minimum*) were included in the analyses as outgroup taxa. Genome assemblies for all species were subjected to BUSCO v. 4.0.5 (Seppey *et al.* 2019) runs using the Sordariomycetes\_odb10 dataset to obtain BUSCO genes. The amino acid sequences were extracted from BUSCO results

and datasets were compiled for each of the BUSCO orthologous groups. All BUSCO orthologous groups with duplicated BUSCO genes were excluded from the analysis. PRANK (Löytynoja 2014) was used to align the datasets with default parameters.

Trimal v. 1.4 (Capella-Gutiérrez *et al.* 2009) was used for trimming of the alignments with “-resoverlap 0.8 -seqoverlap 75” parameters. Only datasets with lengths equal or larger than 100 aa after trimming step were retained for further analysis. Permutation Tail Probability (PTP) tests were conducted in

PAUP v. 4.0a (Swofford 2003) to identify and remove datasets having no phylogenetic signal as well as those with less than 50 parsimony-informative characters. Individual gene trees for each BUSCO orthologous group were constructed using IQ-TREE v. 2 with an optimal substitution model automatically determined and 1 000 ultrafast bootstraps (Hoang *et al.* 2018, Minh *et al.* 2020). TreeShrink v. 1.3.7 (Mai & Mirarab 2018) was used to remove outliers (taxa with abnormal branch length) from all trees with default parameters. Newick utilities (Junier & Zdobnov 2010) was used to collapse branches with less than 10 % bootstrap support. A species tree was then constructed from the final set of trees under the multi-species coalescent model using ASTRAL v. 5.7.7 (Mirarab *et al.* 2014). Branch length of the species tree was optimized with RAxML v. 8.2.11 (Stamatakis 2014) using only BUSCO orthogroups that have all 36 taxa present and without any outlier taxon as identified with TreeShrink analysis.

## Selection of gene regions for phylogenetic analyses

Sequences for eight gene regions commonly used in phylogenetic studies of the fungi were extracted from 31 draft genome sequences for species in the *Ophiostomatales*, as well as from those used as outgroups in the phylogenomic analysis (Supplementary Table S1). These included  $\beta$ -tubulin ( *$\beta$ -tub*), translation elongation factor 1 alpha (*TEF-1 $\alpha$* ), internal transcribed spacer region (ITS), ribosomal large subunit (LSU), mini chromosome maintenance protein complex 7 (*MCM7*), DNA-directed RNA polymerase II second largest subunit (*RPBII*), DNA-directed RNA polymerase II largest subunit (*RPBI*) and ribosomal small subunit (SSU). A phylogenetic tree was constructed for each of these datasets using IQ-TREE v. 2 as indicated above. Based on the level of congruency between individual gene trees and the phylogenomic tree as well as the phylogenetic signal of these gene regions, the LSU, ITS, *TEF-1 $\alpha$*  and *RPBII* gene regions were selected as markers to delineate genera in the *Ophiostomatales*. These regions included the primary (ITS) and secondary (*TEF-1 $\alpha$* ) barcodes for fungi (Schoch *et al.* 2012, Stielow *et al.* 2015).

## Primer selection

Existing primers were used to amplify and sequence the ITS (ITS1F: Gardes & Bruns 1993, ITS4: White *et al.* 1990), *TEF-1 $\alpha$*  (EF2F: Marincowitz *et al.* 2015, EF2R: Jacobs *et al.* 2004) and LSU (LR5, LROR: Vilgalys & Hester 1990) gene regions. Since previously available primers for *RPBII* did not consistently amplify the targeted region in most of the isolates investigated, we designed new primers for this gene region based on the available genome sequences: Oph-RPB2F1 (5' - GAYGAYCGIGAYCAYTTYGG - 3'), Oph-RPB2F2 (5' - TICTGGCIAARCTNTTCCG - 3') and Oph-RPB2R1 (5' - CCCATRGCTGYTTRCCCAT - 3'). A combination of Oph-RPBF1 and Oph-RPBR1 was used in most instances, while Oph-RPBF2 and Oph-RPBR1 were used in cases where the former combination was not successful.

## PCR

For the ITS, *TEF-1 $\alpha$*  and LSU regions, FastStart *Taq* DNA Polymerase (Roche, Germany) was used. For the *RPBII* gene region the Platinum® Multiplex PCR Master Mix (Applied Biosystems, Foster City, California) was used. The ITS, LSU and *TEF-1 $\alpha$*  gene regions were amplified following the protocol described by Duong *et al.* (2012). For the *RPBII* gene region, the protocol provided with

the Platinum® Multiplex PCR Master Mix was used but amended as follows: the PCR mixture was made up to a final volume of 12.5  $\mu$ L, primers were added to a concentration of 1  $\mu$ M each, and PCR was carried out with 40 cycles of denaturing at 94 °C for 30 s, annealing at 58 °C for 30 s, and elongation at 72 °C for 1 min.

Agarose gel electrophoresis (1 % agarose) was performed on all PCR products to confirm the success of amplification. PCR products were treated with ExoSAP (a mixture of exonuclease I and alkaline phosphatase; one unit of each enzyme was used for approximately 20  $\mu$ L of PCR product). The mixture was then subjected to two incubation steps at 37 °C for 15 min (for enzymatic action) and 80 °C for 15 min (to deactivate the enzymes). The treated products were stored at 4 °C until PCR sequencing was carried out.

## DNA sequencing

Sanger sequencing was performed for all ExoSAP treated PCR products. The PCR sequencing setup reaction (12  $\mu$ L) consisted of 6.4  $\mu$ L dH<sub>2</sub>O, 2.1  $\mu$ L 5 $\times$  sequencing buffer, 0.5  $\mu$ L BigDye v 3.1, 1  $\mu$ L of the forward or reverse primer (10 mM), and 2  $\mu$ L ExoSAP treated PCR product. The reaction was performed under the following conditions: 25 cycles of a denaturing step at 96 °C for 10 s, an annealing step at 55 °C for 5 s, and an elongation step at 60 °C for 4 min. The products were maintained at 4 °C until being used for precipitation.

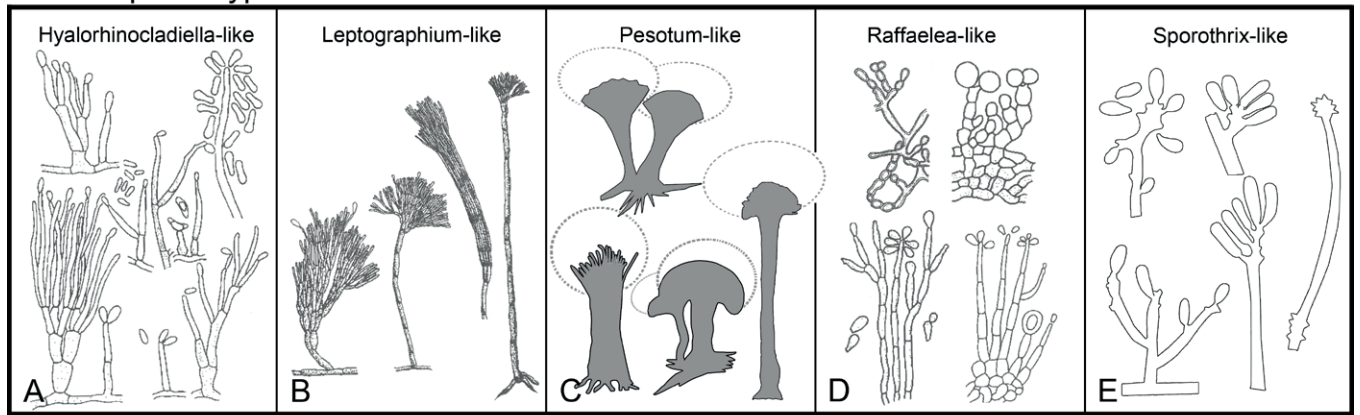
PCR sequencing products were precipitated using the ethanol/NaOAc precipitation method. For each of the PCR sequencing products (total volume of 12  $\mu$ L) 8  $\mu$ L dH<sub>2</sub>O, 2  $\mu$ L NaOAc (3 M, pH 5.2) and 50  $\mu$ L absolute ethanol (EtOH) was added. The tubes were incubated on ice for 10 min, then centrifuged at 13 400 rpm for 30 min at room temperature. After centrifugation, the supernatant was removed, and the pellet washed twice with 150  $\mu$ L of 70 % EtOH and centrifuged for 10 min at 13 400 rpm at room temperature. After the final wash, the supernatant was removed, and the pellet was air-dried for approximately 15 min. The samples were kept at -20 °C until they could be analysed. The fragment separations were performed using an ABI PRISM® 3100 Genetic Analyzer (Applied Biosystems). Consensus sequences were derived from sequences obtained with forward and reverse primers. All sequences generated in this study have been submitted to GenBank, and those from ex-type isolates will be included in the RefSeq Targeted Loci (RTL) database in GenBank (Schoch *et al.* 2014).

## Phylogenetic analyses

For species with available genome sequences (Supplementary Table S1), gene region data were extracted from assembled genome sequences. Sequences were downloaded from GenBank for newly described species for which cultures were not available during the study period, as well as for species for which our sequence data were incomplete. Datasets were aligned using the online version of MAFFT v. 7 (Katoh & Stanley 2013) with default parameters. Alignments were refined with an online version of Gblocks v. 0.91b (Castresana 2000) using default parameters – *i.e.* no alternative options for more or less stringent selection were selected. Datasets for the various gene regions obtained from Gblocks were concatenated using FASconCAT-G (Kück & Meusemann 2010). Partitionfinder v. 2.1.1 (Lanfear *et al.* 2017) was used to determine best substitution models for the combined dataset.

Maximum Likelihood (ML) analyses using RAxML (Stamatakis 2014) were performed separately for all gene regions and for the concatenated dataset with raxmlGUI v. 1.3 (Silvestro & Michalak

Conidiophore types



Ascospore types

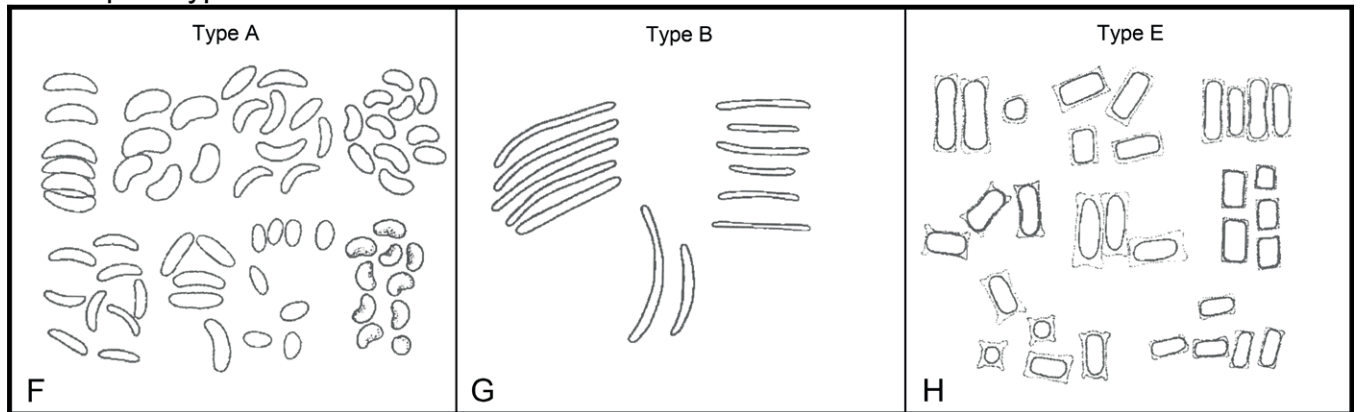


Fig. 3. Conidiophore and ascospore types mentioned in the paper. A–E. Conidiophore types. F–H. Ascospore types *sensu* De Beer & Wingfield (2013). A, B, D, F–H. Adapted from illustrations in De Beer & Wingfield (2013). Shades of grey depict colours of various structures ranging from hyaline to dematiaceous.

2012) using the GTR+G+I substitution model and 1 000 thorough bootstrap replicates. Bayesian analysis was conducted using PhyloBayes-MPI v. 1.8 (Lartillot *et al.* 2013); two chains were run in parallel under the CAT-GTR model. The program bpcmp was used to assess the convergence in tree space. Runs were terminated when the maxdiff value obtained between two chains reached 0.1 or lower.

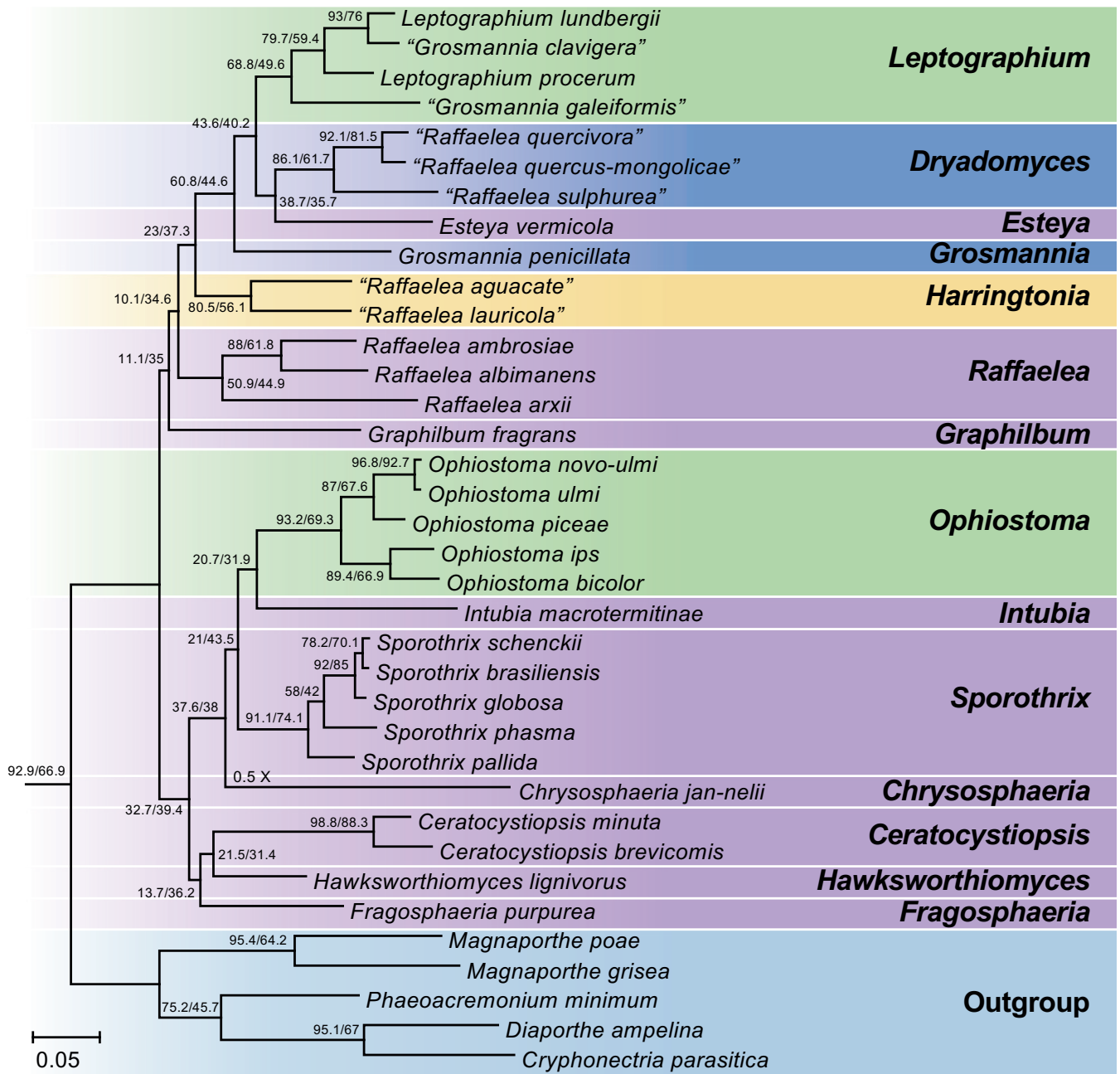
Morphology

Of the 11 ascospore morphotypes defined by De Beer & Wingfield (2013) for the *Ophiostomatales*, three (Type A, B, E) were used to describe ascospore types in the present study (Fig. 3). Type A ascospores are those described as allantoid, bean-shaped, crescent to sickle-shaped, clavate to ovate, curved, cylindrical and slightly curved, orange section, lunate or reniform. Type B ascospores are those that are bacilliform, elongate filiform or narrow clavate. Type E ascospores are those with sheaths and are box-shaped, cylindrical, oblong, pillow-shaped, rectangular or rod-shaped. For the asexual morphs, five conidiophore types, hyalorhinocladiella-like, leptographium-like, pesotum-like, raffaelea-like and sporothrix-like, were used as descriptors where applicable (Fig. 3). Three shades of grey were applied in the figures to depict the colours of structures. Thus, hyaline to subhyaline structures were shaded in pale grey. Brown to dark brown structures were a medium-tone grey and fuscous black to black structures were presented in dark grey.

RESULTS

The phylogenomic tree constructed from the genome-wide sequence data for 31 ophiostomatalean species (Fig. 4) showed a similar topology to those obtained in previous studies (Nel *et al.* 2021, Vanderpool *et al.* 2018). The placement of *Graphilbum fragrans* was, however, different from that suggested by Vanderpool *et al.* (2018). This inconsistent placement for *Gra. fragrans* was also observed by Nel *et al.* (2021) where different phylogenomic approaches were applied. Species of *Leptographium s.l.* grouped in two distinct lineages; one of these accommodated the *Grosmannia penicillata* complex and the other the *L. lundbergii*, *L. procerum* and *L. galeiforme* complexes. Species of *Raffaelea s.l.* resolved in three distinct clades, which is consistent with the findings in two previous studies (Nel *et al.* 2021, Vanderpool *et al.* 2018). Otherwise, all remaining species and genera included in the analysis resided in the clades consistent with their current recognition as separate genera in the *Ophiostomatales*.

The maximum likelihood tree (Fig. 5) resulting from analyses of the concatenated dataset (LSU, ITS, *TEF-1α* and *RPBII*) for 264 isolates representing 249 species revealed 24 distinct lineages. Posterior probability values generated from Bayesian Inference analysis are indicated at the genus-level nodes (Fig. 5). Although the topologies of the individual gene trees (Figs S1–S4) were different to one another and to those in the combined tree, (apart from a few exceptions discussed below), the terminal clades were mostly consistent for the gene regions. To facilitate a discussion of the emerging results, the 24 lineages that represent genera or smaller groups were annotated using Roman numerals (I–XXIV). These were applied in the order of appearance in the

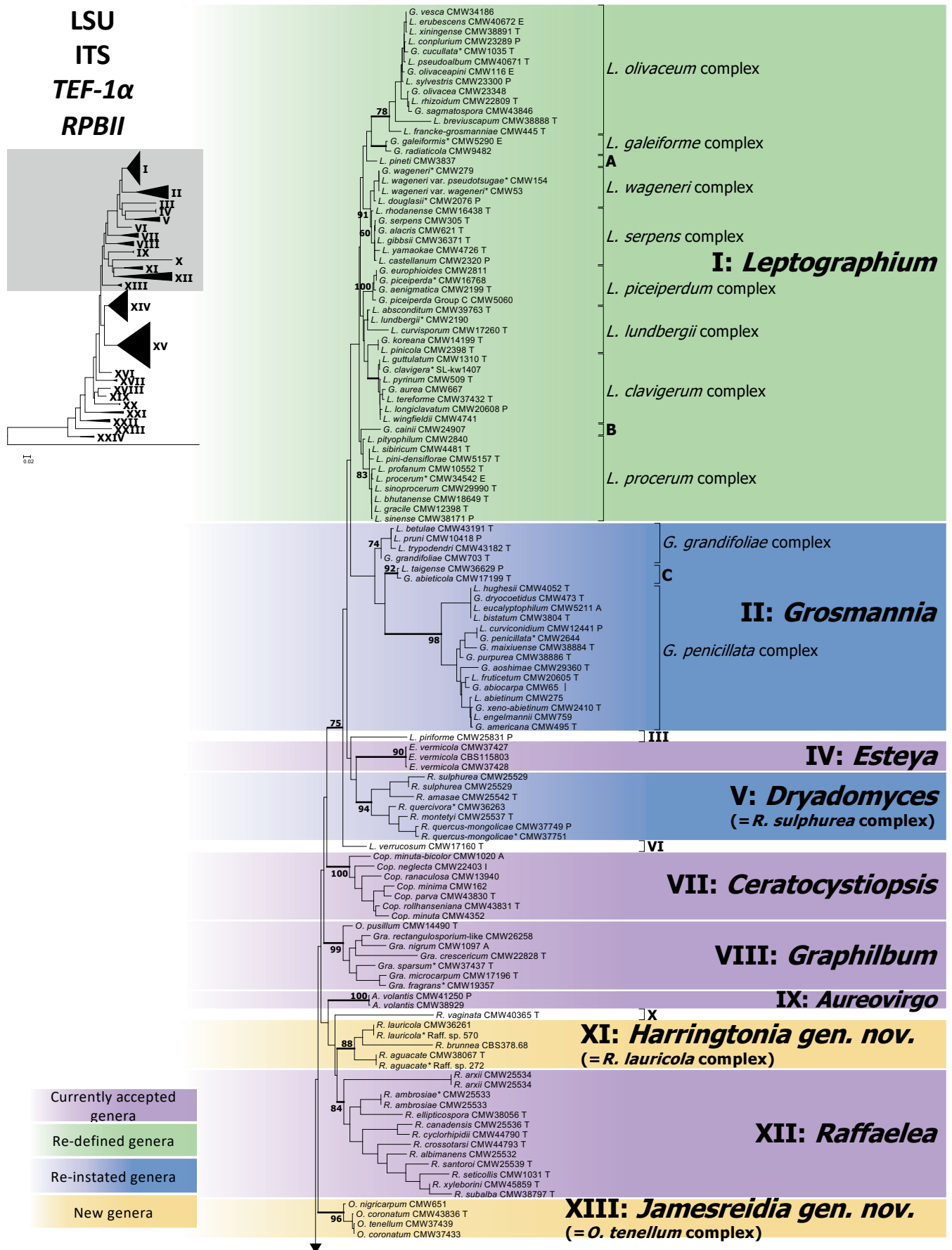


**Fig. 4.** Phylogenomic tree obtained from supertree analysis with ASTRAL using gene trees constructed from 3 548 BUSCO genes (identified using the sordariomycetes\_odb10 dataset; BUSCO v. 4.0.5). All 31 species in the *Ophiostomatales* for which genome sequence currently available were included in the analysis. *Cryphonectria parasitica*, *Diaporthe ampelina*, *Magnaporthe grisea*, *Magnaporthe poae* and *Phaeoacremonium minimum* were included as outgroup taxa. Gene concordance factors (gCF) and site concordance factors (sCF), which indicate the percentage of genes and sites that support a particular nodes respectively, were determined using IQ-TREE2 and are presented at nodes as gCF/sCF. Species names presented in double quotes denote old names which have been changed to their new respective genera subsequent to this study.

concatenated tree (Fig. 5). Single species that grouped within major lineages, but not within defined species complexes, or not consistent within the same lineage in different trees, were labelled alphabetically (A–K).

The overall topology of the LSU tree (Fig. S1) showed some differences from that of the concatenated tree, but 22 of the lineages corresponded between the two trees. The exceptions were Lineages III and XIX. Lineage III consisted of a single species in the concatenated tree, for which no LSU data were available, while Lineage XIX grouped outside the other genera in the concatenated tree, but as part of *Sporothrix* (Lineage XIV) in the LSU tree. Species complexes within *Leptographium*, *Sporothrix* and *Ophiostoma* were generally less well-defined in the LSU tree than in the concatenated tree.

The ITS tree (Fig. S2) showed little resolution below the genus level. Due to the variable nature of the ITS1 and ITS2 regions, the dataset was subjected to a strict Gblocks treatment (using automated parameters). The dataset consisted of 1 132 characters (including gaps) prior to treatment with Gblocks, and only 169 characters thereafter. The remaining dataset on which the tree (Fig. S2) is based, consisted predominantly of the 5.8S region. Nevertheless, we retained this analysis in the study because the ITS region is the officially recognised barcode for the fungi (Schoch *et al.* 2012). The ITS tree (Fig. S2) supported separation of most of the genera, but Lineages XI, XII and XXII were not monophyletic in this tree, when compared to the concatenated tree. The relatively small dataset also failed to resolve most of the species complexes for the larger genera.



**Fig. 5.** Phylogenetic tree depicting the boundaries of currently accepted genera in the *Ophiostomatales*. This tree was generated using maximum likelihood analysis of the concatenated dataset of LSU, ITS, *TEF1- $\alpha$*  and *RPBII* gene regions. The dataset consisted of 264 isolates and 2 360 characters (including gaps). Bootstrap values above 60 % are shown. Bold lines indicate Bayesian posterior probabilities values above 0.8. Bootstrap values and Bayesian posterior probabilities values below the species complex level were removed for simplification. Purple blocks indicate existing genera, yellow blocks new genera described in this study, green blocks, genera that we redefine here, and blue blocks indicate genera that that have been reinstated and re-defined. (T = ex-type, E = ex-epitype, P = ex-paratype; L = ex-lectotype; A = authentic isolate, used in the original study; \* Genome sequenced).



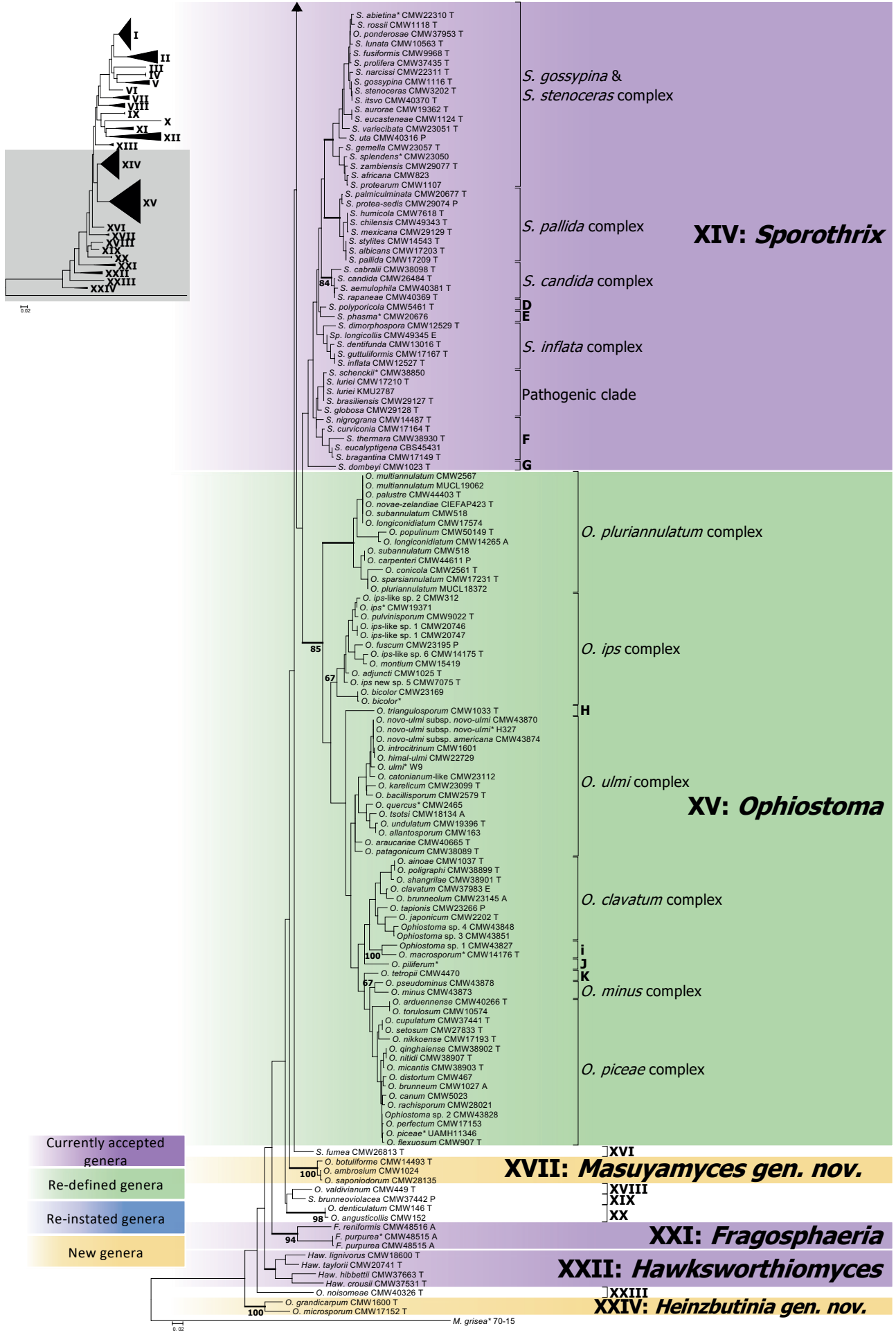


Fig. 5. (Continued).

The *TEF-1 $\alpha$*  tree (Fig. S3) resolved almost all the lineages representing species complexes, but failed to support monophyly of Lineages I, II, VIII, XI and XXII.

The *RPBII* tree (Fig. S4) supported the separation of all genera, species complexes and smaller lineages apart from Lineage XII that separated in four clades, and Lineage VIII that grouped within Lineage I.

Based on the concatenated tree (Fig. 5), Lineage I included species complexes previously defined in *Leptographium s.l.* (De Beer & Wingfield 2013), namely the *Leptographium clavigerum*, *L. galeiforme*, *L. lundbergii*, *L. olivaceum*, *L. piceiperdum*, *L. procerum*, *L. serpens* and *L. wagneri* complexes; as well as two species not forming part of these species complexes (A & B). Lineage II included the *G. grandifoliae* and *G. penicillata* species complexes and a smaller lineage (C). *Leptographium piriforme* was labelled as Lineage III and *L. verrucosum* as Lineage VI, both grouping outside of *Leptographium* (Lineage I). Lineage IV consisted of three isolates of the monotypic genus *Esteya*. The *Raffaelea sulphurea* complex formed Lineage V. *Ceratocystiopsis* spp. formed Lineage VII, *Graphilbum* formed Lineage VIII and *Aureovirgo* formed Lineage IX. *Raffaelea vaginata* grouped outside of *Raffaelea* (Lineage XII) and was labelled Lineage X. Lineage XI consisted of the *R. lauricola* complex, distinct from *Raffaelea* spp., which formed Lineage XII. The *Ophiostoma tenellum* complex formed Lineage XIII. *Sporothrix* and *Ophiostoma*, as defined by De Beer *et al.* (2016a), formed Lineages XIV and XV, respectively. Lineage XIV consisted of the *S. gossypina* and *S. stenoceras* species complexes (which grouped inseparably from each other), the *S. candida*, *S. inflata* and *S. pallida* species complexes, the pathogenic clade (including the type species of *Sporothrix*, *S. schenckii*), as well as groups D to G. Lineage XV included the *O. clavatum*, *O. ips*, *O. minus*, *O. piceae*, *O. pluriannulatum* and *O. ulmi* complexes as well as groups H to K. *Sporothrix fumea* and *S. brunneoviolacea* both grouped separate from *Sporothrix*, and were labelled as Lineages XVI and XIX, respectively. Three *Ophiostoma* species consistently grouped together and distinct from *Ophiostoma* and were labelled Lineage XVII. Lineage XVIII included *O. valdivianum* and Lineage XX consisted of *O. denticulatum* and *O. angusticollis*. Lineage XXI represented *Fragosphaeria*, and Lineage XXII represented *Hawksworthiomyces*. *Ophiostoma noisomeae* was labelled Lineage XXIII, while *O. grandicarpum* and *O. microsporum* together constituted Lineage XXIV.

*Afroraffaelea* was excluded from the final analyses because the placement of the type for this monotypic species, *Afr. ambrosiae*, was completely incongruent among the separate gene trees (data not shown), most often forming long branches, distinct from all other groups. This impacted negatively on the support for several lineages in the concatenated tree, which prompted the decision to exclude the species from the analyses. Likewise, the two species of *Intubia* and the monotypic *Chrysosphaeria* were excluded from the analyses due to their ambiguous generic placement when using traditionally applied phylogenetic markers (Nel *et al.* 2021).

## TAXONOMY

Phylogenetic analyses for four gene regions revealed 16 lineages within the *Ophiostomatales*, which we now recognise as valid genera. Seven of these represent genera currently known and defined in the Order. They include *Esteya* (Lineage IV), *Ceratocystiopsis* (Lineage VII), *Graphilbum* (Lineage VIII), *Aureovirgo* (Lineage IX), *Sporothrix* (Lineage XIV), *Fragosphaeria* (Lineage XXI) and

*Hawksworthiomyces* (Lineage XXII). Two Lineages (Lineage II and V), which were clearly distinct from all other genera, included the ex-type cultures of *Grosmannia penicillata* and *Dryadomyces amasae* respectively. These species have previously been treated in the genera *Grosmannia/Leptographium* and *Raffaelea* respectively and we have consequently reinstated and redefined the genera *Grosmannia* and *Dryadomyces* with emended descriptions. Four lineages (Lineage XI, XIII, XVII and XXIV) are recognised as representing new genera and are described as such. Characters of these new genera were previously included in the descriptions of *Leptographium*, *Ophiostoma* and *Raffaelea*, and we have consequently emended their descriptions. Although *Afroraffaelea*, *Chrysosphaeria*, *Intubia*, and the fossil genus *Paleoambrosia* were not included in our analyses, we recognise these genera as valid, retaining them in the *Ophiostomatales*.

The placement of the remaining lineages (III, VI, X, XVI, XVIII, XIX, XX and XXIII) remains uncertain, as most of these lineages were represented by single species that grouped inconsistently in our analyses. We have chosen not to describe new monotypic genera for these lineages, but rather to delay this decision until additional taxa are discovered that support establishing novel genera. In addition to describing and redefining genera, new combinations have been provided for species where necessary.

## Circumscription of the *Ophiostomatales* and *Ophiostomataceae*

At present there is no need to revise the description of the *Ophiostomatales*. This is because the emended description by De Beer *et al.* (2013a) broadly encompasses the morphologies of all genera, including the novel genera described in the present study. With more than 300 species and clearly distinct broad morphological groups in the Order, it would make sense to provide a narrower definition for the *Ophiostomataceae*, and to introduce one or more additional families. However, in view of the lack of support for the deeper nodes in our analyses, we have refrained from doing so at present. We suggest that this should be done only when related taxa outside the *Ophiostomatales*, such as those included in the LSU and SSU phylogenies of De Beer *et al.* (2013a), can be incorporated in multigene phylogenies to provide more robust context within the *Sordariomycetidae*.

## Currently accepted genera in the *Ophiostomatales*

All currently accepted genera in the *Ophiostomatales* are defined below, and based on our results, descriptions have been emended where necessary. Genera and species complexes are discussed in alphabetical order, with lineage numbers corresponding to their appearance in the concatenated phylogenetic tree (Fig. 5).

## New combinations

Where required, new combinations have been provided, and these are listed under the relevant genera. Species that have been treated in a particular genus but were shown based on our data to reside in a different genus, for which a name already exists in the appropriate genus, have been listed under 'current name' in Table 1, and thus not in the following section. For example, *Grosmannia serpens* is now treated as *Leptographium serpens* but did not require a new combination and is listed in Table 1.

## ***Afroraffaelea* (not included in the phylogenetic analyses)**

***Afroraffaelea*** C.C. Bateman *et al.*, Fungal Ecol. 25: 46. 2017. MycoBank MB 816236. Fig. 6A, B.

**Etymology:** 'Prefix Afro - indicating its likely African origin, and 'raffaelea' to recognise the ecological similarity to the closely related (though probably not monophyletic) ambrosia fungus genus *Raffaelea*' (Bateman *et al.* 2017).

**Sexual morph:** Unknown.

**Asexual morph:** No reproductive structures observed. Colonies white becoming brown with age, aerial hyphae present, abundant, subhyaline, extensively branched often perpendicularly, thickened and melanized intercalarily, distal hyphae denticulate, submerged hyphae subhyaline, constricted at septa, frequently branched, with tapering distal ends, monilloid mycelia occurring in peptone-containing medium, fragmented unicellularly or bicellularly.

**Type species:** *Afroraffaelea ambrosiae* C.C. Bateman *et al.*, Fungal Ecol. 25: 46. 2017. MycoBank MB 816237.

**No other species known.**

**Notes:** *Afroraffaelea* was described by Bateman *et al.* (2017) and has a unique morphology relative to the rest of the *Ophiostomatales*. Within a few days of sub-culturing, *Afr. ambrosiae* (the only species in this genus) produces masses of aerial hyphae, unlike any other ophiostomatalean species, and changes colour from white to brown as the culture matures. The fungus is the dominant fungal symbiont of the ambrosia beetle *Premnobius cavipennis*, presumably introduced into North America from Africa (Bateman *et al.* 2017). The phylogenies of Bateman *et al.* (2017) showed *Afr. ambrosiae* grouping close to *Fragosphaeria*, but there was insufficient phylogenetic support for these authors to determine the taxonomic placement of *Afroraffaelea* in the *Ophiostomatales*.

The taxonomic placement of *Afroraffaelea* in our phylogenetic trees is not conclusive. The four known isolates of *Afr. ambrosiae* consistently grouped together as one species. However, the clade grouped inconsistently in the single gene trees. For example, in the LSU and *TEF-1 $\alpha$*  trees, *Afr. ambrosiae* isolates grouped in Lineage VIII, but with Lineage V in ITS, and with Lineage XXIII in *RPBII* (data not shown). We consequently excluded these isolates from our datasets. We believe that the taxonomic placement of this fungus will be resolved when additional species are found, or possibly with whole genome data. Until such time, we treat *Afroraffaelea* as *incertae sedis* in the *Ophiostomatales*.

## ***Aureovirgo* (Lineage IX)**

***Aureovirgo*** J.A. van der Linde *et al.*, Antonie van Leeuwenhoek 109: 593. 2016. MycoBank MB 813870. Fig. 6C, D.

**Etymology:** 'Refers to the golden appearance of the immature ascomata and the pure white colour of the cultures ("Aureovirgo" refers to a golden maiden with an unstated overtone of virginal whiteness)' (Van der Linde *et al.* 2016).

**Sexual morph:** *Ascomatal bases* subglobose to globose, pale brown when young, becoming darker with age; necks cylindrical,

dark brown. *Ostiolar hyphae* hyaline, parallel. *Ascospores* hyaline, 1-celled, enclosed in a sheath, falcate, endospores (the body of ascospores) allantoid.

**Asexual morph:** Leptographium-like; *conidiophores* macronematous, mononematous, hyaline; *conidiogenous cells* cylindrical, hyaline; *conidia* hyaline, 1-celled, oblong to ellipsoidal.

**Type species:** *Aureovirgo volantis* J.A. van der Linde *et al.*, Antonie van Leeuwenhoek 109: 593. 2016. MycoBank MB 813872.

**No other species known.**

**Notes:** *Aureovirgo* was described from galleries of the ambrosia beetle *Cyrtogenius africanus* in dead and dying *Euphorbia ingens* trees in South Africa. It is a monotypic genus accommodating *A. volantis* (Van der Linde *et al.* 2016). The *ascomatal bases* are honey-coloured when immature, while the rest of the culture is white. This is the only genus in the *Ophiostomatales* associated with *Euphorbia* trees. In our dataset, *Aureovirgo* formed a well-supported, distinct lineage.

## ***Ceratocystiopsis* (Lineage VII)**

***Ceratocystiopsis*** H.P. Upadhyay & W.B. Kendr., Mycologia 67: 799. 1975. MycoBank MB 889. Fig. 6E, F.

**Etymology:** 'Resembling the genus *Ceratocystis*' (Upadhyay & Kendrick 1975, Upadhyay 1981). At the time of the description, Upadhyay & Kendrick (1975) and others treated *Ophiostoma* as a synonym of *Ceratocystis* in the *Ophiostomatales*. *Ceratocystis* was later shown to form part of the *Microascales*, and *Ceratocystiopsis* to be related to *Ophiostoma* in the *Ophiostomatales* (Zipfel *et al.* 2006). Although somewhat of a misnomer, the name *Ceratocystiopsis* remains valid and represents a distinct genus in the *Ophiostomatales*.

**Synonym:** *Hyalorhinocladia* H.P. Upadhyay & W.B. Kendr., Mycologia 67: 800. 1975. MycoBank MB 8582. [Type species *Hyalorhinocladia minuta-bicolor* (R.W. Davidson) H.P. Upadhyay & W.B. Kendr.]

**Sexual morph:** *Ascomatal bases* subglobose, globose, obpyriform, black or pale brown, upper part surrounded with collar-like structure or corona of globose cells; necks short conical to elongate, cylindrical, black or paler than base. *Ostiolar hyphae* absent or present, convergent, parallel, divergent. *Asci* evanescent, clavate, broadly fusiform, 8-spored. *Ascospores* hyaline, 1-celled, enclosed in a sheath, falcate in side view, fusiform, acicular in face view; endospores elongate orange segment-shaped in side view, cylindrical in face view; cucullate, sometimes forming bulbous swelling toward one end.

**Asexual morph:** *Hyalorhinocladia*-like; *conidiophores* micronematous, semimacronematous, macronematous, mononematous, hyaline; *conidiogenous cells* integrate or discrete, polyblastic, sympodial, with denticle scars; *conidia* hyaline, 1-celled, obovoid, ellipsoidal, oval to globose, clavate, T-shaped, Y-shaped, cylindrical.

**Type species:** *Ceratocystiopsis minuta* (Siemaszko) H.P. Upadhyay & W.B. Kendr., Mycologia 67: 800. 1975. MycoBank MB 310480.

**Other species:** Listed in Table 1.

Table 1. Taxa described in the *Ophiostomatales*, based on currently published data.

Previous name	Current name	CMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	GenBank Accession Numbers <sup>3</sup>			
								ITS	LSU	TEF1- $\alpha$	RPBII
<b>Afroraffaelea</b>											
<i>Afr. ambrosiae</i>	<i>Afr. ambrosiae</i>	48331	141678	T	<i>Premnobius cavipennis</i>	Florida, USA	C. Bateman	OM632703	OM584293	OM631576	OM631577
<b>Aureovirgo</b>											
<i>A. volantis</i>	<i>A. volantis</i>	41250	139649	P	<i>Cyrtogenius africanus</i> on <i>Euphorbia ingens</i>	South Africa	J.A. van der Linde	OM501369	OM514700	OM631743	OM631579
<i>A. volantis</i>	<i>A. volantis</i>	38929	140081		<i>Cyrtogenius africanus</i> on <i>Euphorbia ingens</i>	South Africa	J.A. van der Linde	OM501368	OM514699	OM631742	OM631578
<b>Ceratocystiopsis</b>											
<i>Cop. brevicornis</i>	<i>Cop. brevicornis</i>	40952	333.97	T	<i>Dendroctonus brevicornis</i>	California, USA	T. Harrington	EU913722	EU913683	-	-
<i>Cop. collifera</i>	<i>Cop. collifera</i>	7074	126.89	T	<i>Dendroctonus valens</i> on <i>Pinus teocote</i>	Mexico	J. Marmolejo	EU913721	EU913681	-	-
<i>Cop. concentrica</i>	<i>Cop. concentrica</i>	-	WIN(M)71-07		<i>Pinus banksiana</i>	Canada	J. Reid, A. Olchoweki	-	AF135571	-	-
<i>Cop. conicicollis</i>	<i>Cop. conicicollis</i>	-	WIN(M)69-25		<i>Abies balsamea</i>	Canada	J. Reid, A. Olchoweki	-	-	-	-
<i>Cop. longispora</i>	<i>Cop. longispora</i>	-	UM48		<i>Pinus</i> sp.	Canada	A. Olchoweki	EU913723	EU913684	-	-
<i>Cop. lunata</i> <sup>#</sup>	<i>Cop. lunata</i>	55897	47171	T	<i>Xylosandrus crassiusculus</i>	South Africa	W.J. Nel	MW028169	MW028141	-	-
<i>Cop. manitobensis</i>	<i>Cop. manitobensis</i>	13792	UAMH9813	T	Manitoba beetle gallery in <i>Pinus resinosa</i>	Canada	J. Reid	EU913714	EU913674	-	-
<i>Cop. minima</i>	<i>Cop. minima</i>	162	182.86		<i>Pinus banksiana</i>	Wisconsin, USA	M.J. Wingfield	OM501370	OM514701	OM631744	-
<i>Cop. minuta</i> <sup>*</sup>	<i>Cop. minuta</i>	4352	138717		<i>Ips cembrae</i>	Poland	T. Kirisits	OM501372	OM514703	OM631745	OM631581
<i>Cop. minuta-bicolor</i> <sup>*</sup>	<i>Cop. minuta-bicolor</i>	1020	635.66	A	Gallery of <i>Ips</i> sp. in <i>Pinus contorta</i>	USA	R.W. Davidson	OM501371	OM514702	-	OM631580
<i>Cop. neglecta</i>	<i>Cop. neglecta</i>	22403	100596	I	<i>Hylurgops palliatus</i>	Germany	R. Kirschner	OM501373	OM514704	OM631746	OM631582
<i>Cop. ochracea</i>	<i>Cop. ochracea</i>	-	DAOM100148		<i>Picea mariana</i>	Canada	H.D. Griffin	-	-	-	-
<i>Cop. pallidobrunnea</i>	<i>Cop. pallidobrunnea</i>	-	UM51		<i>Populus tremuloides</i>	Canada	J. Reid	-	EU913682	-	-
<i>Cop. parva</i>	<i>Cop. parva</i>	43830	UAMH9650	T	<i>Abies balsamea</i>	Canada	A. Olchoweki	OM501374	-	OM631747	OM631583
<i>Cop. ranaculosa</i>	<i>Cop. ranaculosa</i>	13940	119683		<i>Pinus echinata</i>	North Carolina, USA	F. Hains	OM501375	OM514705	OM631748	OM631584
<i>Cop. rollhanseniana</i>	<i>Cop. rollhanseniana</i>	43831	UAMH9774	T	Unknown beetle on <i>Pinus sylvestris</i>	Norway	J. Reid	OM501376	OM514706	OM631749	-
<i>Cop. spinulosa</i>	<i>Cop. spinulosa</i>	-	DAOM110151	T	<i>Tilia americana</i>	Canada	H.D. Griffin	-	-	-	-
<i>Cop. synnemata</i> <sup>#</sup>	<i>Cop. synnemata</i>	-	NRIF 16918DA	T	<i>Dryocoetes aini</i> infesting <i>Populus tremula</i>	Poland	K. Miskiewicz	MN900988	MN901018	-	-
<i>Cop. yantaiensis</i> <sup>#</sup>	<i>Cop. yantaiensis</i>	-	SNM650	T	<i>Pinus thunbergii</i>	China	R. Chang	MW989411	MZ819924	MZ853080	-
<i>Cop. weihaiensis</i> <sup>#</sup>	<i>Cop. weihaiensis</i>	-	SNM649	T	<i>Pinus thunbergii</i>	China	R. Chang	MW989413	MZ819926	MZ853082	-
<b>Chrysosphaeria</b>											
<i>Chr. jan-nelii</i> <sup>#</sup>	<i>Chr. jan-nelii</i>	47058	141570	T	<i>Termitomyces</i> fungal comb of <i>Macrotermes natalensis</i>	South Africa	W.J. Nel	MT637038	MT637006	-	-
<b>Dryadomyces (R. sulphurea complex)</b>											
<i>R. amasae</i>	<i>D. amasae</i>	25542	116694	T	<i>Amasa conciliatus</i> on Angiosperms	Taiwan	H. Gebhardt	-	MT629750	OM631750	OM631585
<i>R. montelyi</i>	<i>D. montelyi</i>	25537	463.94	T	<i>Platyplus cylindrus</i> on <i>Quercus suber</i>	France	D. Vouland	-	MT629761	OM631751	-
<i>R. quercivora</i> <sup>*</sup>	<i>D. quercivorus</i>	36263	122982		<i>Quercus mongolica</i>	Japan	T. Kubono	MT633072	MT629762	OM631752	OM631586
<i>R. quercus-mongolicae</i>	<i>D. quercus-mongolicae</i>	37749	KACC44403	P	<i>Quercus mongolica</i>	South Korea	K.H. Kim	MT633073	MT629764	OM631754	OM631588
<i>R. quercus-mongolicae</i> <sup>*</sup>	<i>D. quercus-mongolicae</i>	37751	KACC44405		<i>Platyplus koryoensis</i> -infested <i>Quercus</i>	South Korea	K.H. Kim	MT633074	MT629763	OM631753	OM631587
<i>R. sulphurea</i> <sup>*</sup>	<i>D. sulphureus</i>	25529	380.68		<i>Xyleborus saxesenii</i> gallery in <i>Populus deltoides</i>	Kansas, USA	L.R. Batra	MT633077	MT629768	OM631755	OM631589

Table 1. (Continued).

Previous name	Current name	CMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	GenBank Accession Numbers <sup>3</sup>			
								ITS	LSU	TEF1- $\alpha$	RPBII
<b>Esteya</b>											
<i>E. vermicola</i>	<i>E. vermicola</i>	37427	100821		<i>Olea europaea</i>	Italy	S. Frisullo	-	OM514708	OM631757	OM631591
<i>E. vermicola</i>	<i>E. vermicola</i>	37428	156.82		<i>Pinus</i> sp.	Taiwan	T. Tatsuno	OM501378	OM514709	OM631758	-
<i>E. vermicola</i>	<i>E. vermicola</i>	-	115803		<i>S. intricatus</i> and its galleries in oak trees	Czech Republic	L. Marvanova	OM501377	OM514707	OM631756	OM631590
<b>Fragosphaeria</b>											
<i>F. purpurea</i>	<i>F. purpurea</i>	48515	133.34	A	<i>Fagus</i> sp.	England, UK	C.G.C. Chesters	OM501379	OM514710	OM631759	OM631592
<i>F. reniformis</i>	<i>F. reniformis</i>	48516	134.34	A	<i>Fagus</i> sp.	England, UK	E.W. Mason	OM501381	-	OM631760	OM631593
<b>Graphilbum</b>											
<i>Gra. acuminatum</i> <sup>#</sup>	<i>Gra. acuminatum</i>	54769	145828	T	<i>Ips acuminatus</i> gallery on <i>Pinus sylvestris</i>	Poland	R. Jankowiak	MN548902	-	MN548952	-
<i>Gra. brunneocrinium</i>	<i>Gra. brunneocrinium</i>	-	TRTC34581	T	<i>Abies balsamea</i>	Canada	-	-	-	-	-
<i>Gra. carpaticum</i> <sup>#</sup>	<i>Gra. carpaticum</i>	43141	145835	T	<i>Pissodes piceae</i> gallery on <i>Abies alba</i>	Poland	P. Majka	KY568116	-	MN548956	-
<i>Gra. curvidentis</i> <sup>#</sup>	<i>Gra. curvidentis</i>	54779	145832	T	<i>Pitokteines curvidens</i> gallery on <i>Abies alba</i>	Poland	P. Bilanski	KY568111	-	KY568850	-
<i>Gra. crescericum</i>	<i>Gra. crescericum</i>	22828	130864	T	<i>Hylurgops palliatus</i> on <i>Pinus radiata</i>	Spain	P. Romon	OM501403	OM514749	OM631779	OM631604
<i>Gra. curvicolle</i>	<i>Gra. curvicolle</i>	-	WIN(M)70-25	T	<i>Abies balsamea</i>	Canada	J. Reid, A. Olchoweki	-	-	-	-
<i>Gra. fragrans</i> <sup>#</sup>	<i>Gra. fragrans</i>	19357	138720	T	<i>Pinus patula</i>	South Africa	X.D. Zhou	OM501404	OM514750	OM631780	OM631605
<i>Gra. funicola</i> <sup>#</sup>	<i>Gra. funicola</i>	44770	145813	T	<i>Tomicus piniperda</i> in <i>Pinus sylvestris</i>	Norway	R.H. Lindseith, T.H. Sundt	MN548907	-	MN548961	-
<i>Gra. gorcense</i> <sup>#</sup>	<i>Gra. gorcense</i>	34153	146203	T	<i>Tetropium</i> sp. in <i>Picea abies</i>	Poland	R. Jankowiak	MN548919	-	MN548972	-
<i>Gra. interstitiale</i> <sup>#</sup>	<i>Gra. interstitiale</i>	54780	145816	T	<i>Hylurgops interstitialis</i> in <i>Pinus sylvestris</i>	Russia	H. Solheim	MN548909	-	MN548963	-
<i>Gra. ipis-grandicollis</i> <sup>#</sup>	<i>Gra. ipis-grandicollis</i>	-	VPR43762	T	<i>Ips grandicollis</i> gallery on <i>Pinus radiata</i>	Australia	A.J. Carnegie	MW046071	MW046117	MW066405	-
<i>Gra. kesiyae</i>	<i>Gra. kesiyae</i>	41729	139652	T	<i>Polygraphus szrnaoensis</i> on <i>Pinus kesiya</i>	China	S. Taerum	MG205669	-	-	-
<i>Gra. microcarpum</i>	<i>Gra. microcarpum</i>	17196	YCC439	T	<i>Cryphalus montanus</i>	Japan	Y. Yamaoka	OM501405	OM514751	OM631781	OM631606
<i>Gra. nigrum</i>	<i>Gra. nigrum</i>	1097	163.61	A	<i>Abies lasiocarpa</i>	Colorado, USA	R.W. Davidson	OM501406	OM514752	-	OM631607
<i>Gra. niveum</i> <sup>#</sup>	<i>Gra. niveum</i>	-	SNM145	T	<i>Pinus thunbergii</i>	China	R. Chang	MW989418	-	MZ019548	-
<i>Gra. puerense</i>	<i>Gra. puerense</i>	41673	139640	T	<i>Ips acuminatus</i> on <i>Pinus kesiya</i>	China	S. Taerum	MG205671	-	-	-
<i>Gra. rectangulosporium</i>	<i>Gra. rectangulosporium</i>	29364	MAFF 238952	T	<i>Polygraphus proximus</i> on <i>Abies mariesii</i>	Japan	N. Ohtaka	MG205671	-	-	-
<i>Gra. roseum</i> <sup>#</sup>	<i>Gra. roseum</i>	40349	141074	T	<i>Curtisia dentata</i>	South Africa	T. Musvuugwa	KY050751	-	-	-
<i>Gra. sexdentatum</i> <sup>#</sup>	<i>Gra. sexdentatum</i>	54773	145814	T	<i>Ips sexdentatus</i> in <i>Pinus sylvestris</i>	Norway	H. Solheim, M.E. Waalberg	MN548915	-	MN548968	-
<i>Gra. sparsum</i> <sup>#</sup>	<i>Gra. sparsum</i>	37437	405.77	T	Bark beetle gallery on <i>Picea glauca</i>	Alaska, USA	R.W. Davidson	OM501409	OM514755	-	OM631608
<i>Gra. translucens</i> <sup>#</sup>	<i>Gra. translucens</i>	-	SNM144	T	<i>Pinus thunbergii</i>	China	R. Chang	MW989416	-	MZ019546	-
<i>Gra. tsugae</i>	<i>Gra. tsugae</i>	-	UAMH11701	T	<i>Tsuga heterophylla</i>	Canada	J. Reid, B. Reid	KJ661745	-	-	-
<i>Gra. tubicolle</i>	<i>Gra. tubicolle</i>	43837	UAMH9686	T	<i>Pinus banksiana</i>	Canada	A. Olchoweki	-	-	-	-
<i>O. pusillum</i>	<i>Gra. pusillum</i>	14490	-	T	<i>Pinus densiflora</i>	Japan	H. Masuya	OM501407	OM514753	-	-
<b>Grosmannia: G. penicillata complex</b>											
<i>G. abiocarpa</i>	<i>G. abiocarpa</i>	65	594.85	L	<i>Ips</i> sp. on <i>Picea engelmannii</i>	Colorado, USA	R.W. Davidson	OM501384	OM514715	OM631764	-

Table 1. (Continued).

Previous name	Current name	CMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	ITS	LSU	TEF1- $\alpha$	RPBII	
<i>G. americana</i>	<i>G. americana</i>	495	497.96	T	<i>Dendroctonus simplex</i> on <i>Larix laricina</i>	Vermont, USA	D. Bergdahl	OM501385	OM514718	OM631765	OM631595	
<i>G. aoshimae</i>	<i>G. aoshimae</i>	29360	MAFF238948	T	<i>Polygraphus proximus</i> on <i>Abies mariesii</i>	Japan	N. Ohtaka	OM501386	OM514719	OM631766	OM631596	
<i>G. crassifolia</i> <sup>#</sup>	<i>G. crassifolia</i>	38885	136505	T	<i>Polygraphus poligraphus</i> in <i>Pinus crassifolia</i>	China	X.D. Zhou, S. Taerum	-	MN644475	MN647897	-	
<i>G. dryocoetis</i>	<i>G. dryocoetis</i>	473	376.66	T	<i>Dryocoetes confusus</i> on <i>Abies lasiocarpa</i>	Canada	A.C. Molnar	OM501392	OM514727	OM631768	OM631597	
<i>L. fenglinhense</i>	<i>G. fenglinhense</i>	44579	141896	T	<i>Ips typographus</i> on <i>Pinus</i> sp.	China	R. Chang, S.F. Chen	MH144128	-	MH124404	-	
<i>G. maixiuense</i>	<i>G. maixiuense</i>	38884	136502	T	<i>Polygraphus poligraphus</i> , <i>Ips shangrila</i> in <i>Picea crassifolia</i>	China	M. Yin, S. Taerum, X.D. Zhou	OM501396	MN644474	MN647900	OM631599	
<i>G. penicillata</i> <sup>*</sup>	<i>G. penicillata</i>	2644	116008	T	<i>Picea abies</i>	Norway	H. Solheim	OM501397	OM514737	OM631774	OM631600	
<i>G. purpurea</i>	<i>G. purpurea</i>	38886	136975	T	<i>Ips shangrila</i> on <i>Picea purpurea</i>	China	M. Yin, S. Taerum, X.D. Zhou	OM501399	MN644476	MN647914	-	
<i>G. tibetensis</i>	<i>G. tibetensis</i>	-	CFCC53415	T	<i>Orthotomicus</i> sp. on <i>Pinus likiangensis</i> var. <i>balfouriana</i>	Tibet	Z. Wang, Q. Lu	MT269759	-	MT268756	-	
<i>G. xeno-abietinum</i>	<i>G. xeno-abietinum</i>	2410	136514	T	<i>Pinus ponderosa</i>	California, USA	T. Harrington	OM501402	MN644471	MN647894	OM631603	
<i>G. xianmiense</i> <sup>#</sup>	<i>G. xianmiense</i>	38892	136500	T	<i>Polygraphus poligraphus</i> in <i>Pinus crassifolia</i>	China	X.D. Zhou, S. Taerum	-	MN644479	MN647911	-	
<i>G. zekuensis</i> <sup>#</sup>	<i>G. zekuensis</i>	41876	141901	T	<i>Bakeriana</i> sp. in gallery of <i>Ips nitidus</i> on <i>Picea crassifolia</i>	China	S.J. Taerum	MH121683	MH121683	MH124546	-	
<i>L. abieticolens</i>	<i>G. abieticolens</i>	2865	115248	T	<i>Abies balsamea</i>	Vermont, USA	D. Bergdahl	AF343701	-	-	-	
<i>L. abietinum</i>	<i>G. abietina</i>	275	118590	T	<i>Picea engelmannii</i>	Canada	A. Molnar	OM501383	OM514713	OM631763	OM631594	
<i>L. altius</i>	<i>G. altior</i>	12471	123619	T	<i>Picea koratensis</i>	China	X.D. Zhou, Z.W. de Beer	HQ406851	-	HQ406875	-	
<i>L. bistatum</i>	<i>G. bistata</i>	3804	120192	T	<i>Pinus radiata</i>	Japan	J.J. Kim	OM501388	OM514721	OM631795	-	
<i>L. chlamydatum</i>	<i>G. chlamydata</i>	36631	128840	T	<i>Pityogenes chalcographus</i> on <i>Picea abies</i>	Finland	Z.W. de Beer	JF279965	-	JF280080	-	
<i>L. curviconidium</i>	<i>G. curviconidia</i>	12441	123617	P	<i>Ips typographus</i> on <i>Picea koratensis</i>	China	X.D. Zhou, Z.W. de Beer	OM501390	OM514725	OM631767	-	
<i>L. curvisporum</i>	<i>G. curvispora</i>	17260	123914	T	<i>Picea abies</i>	Norway	M.J. Wingfield, H. Solheim	OM501391	OM514726	EU979347	-	
<i>L. engelmannii</i>	= <i>G. abietina</i>	759	-		<i>Picea engelmannii</i>	Canada	R.W. Davidson	-	OM631763	OM631762	-	
<i>L. eucalyptophilum</i>	<i>G. eucalyptophila</i>	5211	-	A	<i>Eucalyptus urophylla</i> × <i>E. pellita</i>	Democratic Republic of Congo	J. Roux	OM501393	OM514728	OM631769	-	
<i>L. euphyes</i>	<i>G. euphyes</i>	259	109701	T	<i>Pinus strobus</i>	New Zealand	M. Dick	AF343686	-	-	-	
<i>L. fruticetum</i>	<i>G. fruticetum</i>	20605	-	T	<i>Picea engelmannii</i> × <i>P. glauca</i>	Canada	S. Massoumi Alamouti	OM501394	OM514730	OM631770	-	
<i>L. hughesii</i>	<i>G. hughesii</i>	4052	109709	T	<i>Aquilaria</i> sp.	Vietnam	B. Lanchette	OM501395	OM514732	OM631772	OM631598	
<i>L. pistaciae</i>	<i>G. pistaciae</i>	12499	123626	T	<i>Pistacia chinensis</i>	China	X.D. Zhou, Z.W. de Beer	HQ406846	-	HQ406870	-	
<b>Grossmannia: <i>G. grandifoliae</i> complex</b>												
<i>G. grandifoliae</i>	<i>G. grandifoliae</i>	703	ATCC28746	T	<i>Fagus grandifolia</i>	Iowa, USA	R.W. Davidson	-	-	OM631771	-	
<i>L. betulae</i>	<i>G. betulae</i>	43191	142734	T	<i>Scolytus ratzeburgi</i> on <i>Betula verrucosa</i>	Poland	R. Jankowiak	KY801840	-	KY801817	-	

Table 1. (Continued).

Previous name	Current name	CIMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	GenBank Accession Numbers <sup>3</sup>			
								ITS	LSU	TEF1- $\alpha$	RPBII
<i>L. pruni</i>	<i>G. pruni</i>	10418	120197	P	<i>Polygraphus ssiorei</i> on <i>Prunus jamasakura</i>	Japan	H. Masuya	OM501398	OM514740	OM631775	-
<i>L. trypodendri</i>	<i>G. trypodendri</i>	43182	142724	T	<i>Trypodendron domesticum</i> on <i>Fagus sylvatica</i>	Norway	R. Jankowiak	KY801828	-	KY801805	-
<b>Grossmannia: Group C</b>											
<i>G. abieticola</i>	<i>G. abieticola</i>	17199	-	T	<i>Dryocoetes hectographus</i> on <i>Abies mariesii</i>	Japan	Y. Yamaoka	OM501382	OM514712	OM631761	-
<i>L. innermongolica</i>	<i>G. innermongolica</i>	-	MUCL55158	T	<i>Ips subelongatus</i> on <i>Larix</i> sp.	China	Q. Lu	KM236107	-	KM981763	-
<i>L. taigense</i>	<i>G. taigense</i>	36629	-	P	<i>Ips typographus</i> on <i>Picea abies</i>	Russia	Z.W. de Beer	OM501400	OM514744	OM631777	-
<i>L. gestamen</i>	<i>G. gestamen</i>	38096	CIEFAP453	T	<i>Nothofagus dombeyi</i>	Argentina	A. de Estrasi	KT362234	KT362232	KT381300	-
<b>Harringtonia gen. nov. (previously <i>Raffalea lauricola</i> complex)</b>											
<i>R. aguacate</i>	<i>Har. aguacate</i>	38067	141672	T	<i>Persea americana</i>	Florida, USA	C.L. Harmon	-	KJ909296	-	-
<i>R. aguacate</i>	<i>Har. aguacate</i>	-	Raff. sp. 272	T	<i>Persea americana</i>	Florida, USA	C.L. Harmon	MT633065	MT629748	OM631783	OM631613
<i>R. brunnea</i>	<i>Har. brunnea</i>	-	378.68	T	<i>Monarthrum</i> sp.	USA	L.R. Batra	-	EU177457	-	-
<i>R. lauricola</i>	<i>Har. lauricola</i>	-	Raff. sp. 570	T	<i>Xyleborus</i> sp. on <i>Persea</i> sp.	Florida, USA	J. Smith	MT633071	MT629759	OM631784	OM631614
<i>R. lauricola</i>	<i>Har. lauricola</i>	36261	PL159	T	<i>Xyleborus glabratus</i>	Georgia, USA	S. Fraedrich	OM501411	MT629760	OM631785	OM631615
<b>Hawksworthiomyces</b>											
<i>Haw. crousii</i>	<i>Haw. crousii</i>	37531	MUCL55928	T	Bamboo chips	South Korea	J.J. Kim	KX396551	KX396548	OM652622	OM631609
<i>Haw. hibbettii</i>	<i>Haw. hibbettii</i>	37663	MUCL55929	T	<i>Trachymyrmex</i> sp.	Texas, USA	U. Mueller	KX396550	KX396547	OM652623	OM631610
<i>Haw. lignivorus</i>	<i>Haw. lignivorus</i>	18600	119148	T	<i>Eucalyptus</i> pole	South Africa	E.M. de Meyer	OM501410	OM514756	OM631782	OM631611
<i>Haw. taylorii</i>	<i>Haw. taylorii</i>	20741	MUCL55927	T	<i>Eucalyptus</i> pole	South Africa	E.M. de Meyer	KX396549	KX396546	OM652624	OM631612
<i>'Haw. sequentia</i> ENAS'	<i>'Haw. sequentia</i> ENAS'	-	nik62104a_03C_19	T	<i>Picea</i> log	Sweden	-	HQ611296	-	-	-
<b>Heinzbutinia gen. nov.</b>											
<i>O. grandicarpum</i>	<i>He. grandicarpa</i>	1600	250.88	T	<i>Quercus robur</i>	Poland	H. Butin	OM501412	OM514757	OM631786	OM631616
<i>O. longicollum</i>	<i>He. longicolla</i>	-	JCM10198	T	<i>Quercus mongolica</i> var. <i>grosseserrata</i> infested by <i>Platypus quercivorus</i>	Japan	H. Masuya	-	-	-	-
<i>O. microsporum</i>	<i>He. microspora</i>	17152	440.69	T	<i>Quercus</i> sp.	Virginia, USA	R.W. Davidson	-	OM514758	OM631787	OM631617
<i>O. solheimii</i>	<i>He. solheimii</i>	52050	144881	T	<i>Anisandrus dispar</i> infesting <i>Quercus robur</i>	Poland	P. Wieczorek	MH283134	-	MH283488	-
<b>Intubia</b>											
<i>I. macrotermittinarum</i>	<i>I. macrotermittinarum</i>	46496	141560	T	<i>Termitomyces</i> fungal comb of <i>Macrotermes natalensis</i>	South Africa	W.J. Nel	MT637025	-	-	-
<i>I. oerfemansii</i>	<i>I. oerfemansii</i>	47048	141564	T	<i>Termitomyces</i> fungal comb of <i>Macrotermes natalensis</i>	South Africa	W.J. Nel	MT637024	-	-	-
<b>Jamesreidia gen. nov. (previously <i>O. tenellum</i> complex)</b>											
<i>O. coronatum</i>	<i>J. coronata</i>	43836	UAMH9685	T	<i>Pinus</i> sp.	Canada	A. Oichowecki	OM501413	OM514759	OM631788	OM631618
<i>O. nigricarpum</i>	<i>J. nigricarpa</i>	651	638.66	T	<i>Pseudotsuga menziesii</i>	Idaho, USA	R.W. Davidson	AY280490	DQ294356	-	-
<i>O. rostricoronata</i>	<i>J. rostricoronata</i>	456	434.77	T	Pulpwood chips	Wisconsin, USA	R.W. Davidson	AY194509	KX590871	-	-
<i>O. tenellum</i>	<i>J. tenella</i>	37439	189.86	T	<i>Pinus</i> sp.	Colorado, USA	R.W. Davidson	OM501414	OM514760	OM631789	-
<b>Leptographium: L. clavigerum complex</b>											
<i>G. aurea</i>	<i>L. aureum</i>	667	438.69	A	<i>Pinus contorta</i> var. <i>latifolia</i>	Canada	R. W. Davidson	OM501387	OM514720	OM631793	OM631621

Table 1. (Continued).

Previous name	Current name	CMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	ITS	LSU	TEF1- $\alpha$	RPBII	
<i>G. clavigera</i> <sup>3</sup>	<i>L. clavigerum</i>	-	SL-Kw1407		Sapwood associated with <i>Dendroctonus ponderosae</i>	Canada	S. Lee	OM501421	OM514723	OM631799	OM631624	
<i>G. robusta</i>	<i>L. robustum</i>	668	-	T	<i>Pinus ponderosa</i>	Idaho, USA	R.C.R. Jeffrey, R.W. Davidson	-	AY544619	JF798465	-	
<i>L. longiclavatum</i>	<i>L. longiclavatum</i>	20608	-	P	<i>Pinus contorta</i>	Canada	S. Lee	-	OM514771	-	-	
<i>L. pyrinum</i>	<i>L. pyrinum</i>	509	120181	T	<i>Dendroctonus adjunctus</i>	USA	R.W. Davidson	OM501445	OM514781	OM631819	OM631642	
<i>L. terebrantis</i>	<i>L. terebrantis</i>	29841	337.70	T	<i>Dendroctonus terebrantis</i>	Louisiana, USA	S.J. Baras	JF798477	-	JF798470	-	
<i>L. teretiforme</i>	<i>L. teretiforme</i>	37432	125736	T	<i>Hylurgus ligniperda</i>	California, USA	S.J. Kim	OM501455	OM514786	OM631828	OM631649	
<i>L. wingfieldii</i>	<i>L. wingfieldii</i>	4741	-		<i>Pinus densiflora</i>	Japan	H. Masuya	OM501461	OM514789	OM631834	OM631654	
<b>Leptographium: L. galeiforme complex</b>												
<i>G. galeiformis</i> <sup>3</sup>	<i>L. galeiforme</i>	5290	115711	E	<i>Pinus sylvestris</i>	Scotland	T. Kiritsis	OM501428	OM514731	OM631806	OM631631	
<i>G. radiaticola</i>	<i>L. radiaticola</i>	9482	-		<i>Hylurgus ligniperda</i> on <i>Pinus radiata</i>	Chile	X.D. Zhou	OM501446	OM514742	OM631820	OM631643	
<i>L. doddsii</i> <sup>#</sup>	<i>L. doddsii</i>	34479	143470	T	<i>Dendroctonus valens</i>	California, USA	M.J. Wingfield	MT637215	MT637212	MT637205	-	
<i>L. gordonii</i> <sup>#</sup>	<i>L. gordonii</i>	34619	143477	T	<i>Dendroctonus valens</i> in <i>Pinus resinosa</i>	New Hampshire, USA	M.J. Wingfield	MT637226	MT637213	MT637207	-	
<i>L. koraiense</i>	<i>L. koraiense</i>	44461	141898	T	<i>Ips typographus</i> on <i>Pinus koraiensis</i>	China	R. Chang	MH144096	-	MH124372	-	
<i>L. owenii</i> <sup>#</sup>	<i>L. owenii</i>	34448	143467	T	<i>Dendroctonus valens</i>	California, USA	M.J. Wingfield	MT637217	KF515912.1	KF515884.1	-	
<i>L. seifertii</i> <sup>#</sup>	<i>L. seifertii</i>	34620	143478	T	<i>Dendroctonus valens</i> on <i>Pinus resinosa</i>	New Hampshire, USA	M.J. Wingfield	MT637224	KF515911.1	KF515885.1	-	
<b>Leptographium: L. lundbergii complex</b>												
<i>G. koreana</i>	<i>L. koreanum</i>	14199	KUC2078	T	<i>Tomicus piniperda</i> on <i>Pinus koraiensis</i>	South Korea	J.J. Kim	OM501431	OM514733	OM631808	OM631633	
<i>G. yunnanensis</i>	<i>L. yunnanense</i>	5152	-		<i>Pinus yunnanensis</i>	China	X.D. Zhou	AY707207	-	-	-	
<i>L. absconditum</i>	<i>L. absconditum</i>	39763	136527	T	<i>Orthotomicus laricis</i> on <i>Pinus nigra</i>	Spain	P. Romon	OM501415	OM514761	OM631790	-	
<i>L. celere</i>	<i>L. celere</i>	12422	123628	T	<i>Pinus sennanensis</i>	China	X.D. Zhou, Z.W. de Beer	HQ406834	-	HQ406858	-	
<i>L. conjunctum</i>	<i>L. conjunctum</i>	12473	123631	T	<i>Pinus yunnanensis</i>	China	X.D. Zhou, Z.W. de Beer	HQ406831	-	HQ406855	-	
<i>L. lundbergii</i>	<i>L. lundbergii</i>	2190	138716		<i>Pinus sylvestris</i>	Norway	H. Roll-Hansen	OM501432	OM514772	OM631809	OM631634	
<i>L. manifestum</i>	<i>L. manifestum</i>	12436	123622	T	<i>Larix olgensis</i>	China	X.D. Zhou, Z.W. de Beer	HQ406839	-	HQ406863	-	
<i>L. pinicola</i>	<i>L. pinicola</i>	2398	-	T	<i>Hylastes</i> sp. on <i>Pinus</i> sp.	Canada	J. Juzwik	OM501439	OM514775	-	-	
<i>L. shansheni</i>	<i>L. shansheni</i>	44462	141895	T	<i>Ips typographus</i> on <i>Picea</i> sp.	China	R. Chang, S.F. Chen	MH144097	-	MH124373	-	
<i>L. sosnaicola</i> <sup>#</sup>	<i>L. sosnaicola</i>	52084	147023	T	<i>Pinus sylvestris</i>	Poland	D. Jazłowiecka	MT210337	MT210353	MT210397	-	
<i>L. truncatum</i>	<i>L. truncatum</i>	28	929.85	T	<i>Pinus taeda</i>	South Africa	M.J. Wingfield	DQ062052/AY935626	-	DQ062019	-	
<i>L. wushanense</i>	<i>L. wushanense</i>	-	YMF1.04936	T	<i>Pinus</i> sp.	China	J. Lu	MG878407	-	MG878409	-	
<b>Leptographium: L. olivaceum complex</b>												
<i>G. cucullata</i>	<i>L. cucullatum</i>	1035	218.83	T	<i>Ips typographus</i>	Norway	H. Solheim	OM501423	OM514724	OM631801	OM631626	
<i>G. davidsonii</i>	<i>L. davidsonii</i>	-	YCC611		Logs of <i>Larix kaempferi</i> infested with <i>Ips subelongatus</i>	Japan	Y. Yamaoka	GU134165	-	-	-	



Table 1. (Continued).

Previous name	Current name	CMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	GenBank Accession Numbers <sup>3</sup>			
								ITS	LSU	TEF1- $\alpha$	RPBII
<i>G. olivacea</i>	<i>L. olivaceum</i>	23348	-		<i>Pinus sylvestris</i>	Finland	Z.W. de Beer, P. Niemeiä	OM501434	OM514735	OM631811	-
<i>G. olivaceapini</i>	<i>L. olivaceapini</i>	116	504.86	E	<i>Pinus ponderosa</i> in <i>Dendroctonus</i> sp.	Arizona, USA	T. Hinds	OM501433	OM514736	OM631810	OM631635
<i>G. sagmatospora</i>	<i>L. sagmatosporum</i>	43846	UAMH6971		<i>Pinus strobus</i>	Canada	B. Grylls, K. Seifert	OM501449	OM514743	OM631823	-
<i>G. vesca</i>	<i>L. vescum</i>	34186	800.73		<i>Ips pilifrons</i> , <i>Dendroctonus engelmannii</i> in <i>Picea engelmannii</i>	Colorado, USA	F.F. Lombard, R. W. Davidson	OM501457	OM514745	-	-
<i>L. brevicolle</i>	<i>L. brevicolle</i>	-	150.78		Beele gallery in <i>Populus tremuloides</i>	Colorado, USA	R.W. Davidson	MH055549	AF155670	MH055635	-
<i>L. breviuscapum</i>	<i>L. breviuscapum</i>	38888	136507	T	<i>Picea crassifolia</i> infested with <i>Polygraphus poligraphus</i>	China	M.L. Yin, X.D. Zhou	OM501419	OM514763	MN517742	-
<i>L. conplurium</i>	<i>L. conplurium</i>	23289	128834	P	<i>Pinus sylvestris</i>	Finland	Z.W. de Beer, P. Niemeiä	OM501422	OM514765	OM631800	OM631625
<i>L. duchongi</i>	<i>L. duchongi</i>	44455	141897	T	<i>Ips typographus</i> on <i>Pinus koraiensis</i>	China	R. Chang	MH144122	-	MH124398	-
<i>L. erubescens</i>	<i>L. erubescens</i>	40672	278.54	E	<i>Pinus sylvestris</i>	Sweden	A. Mathiesen-Käärik	OM501425	OM514767	OM631803	OM631628
<i>L. flavum</i>	<i>L. flavum</i>	51797	144099	T	<i>Quercus robur</i>	Poland	R. Jankowiak	MH055548	-	MH055634	-
<i>L. francke-grosmanniae</i>	<i>L. francke-grosmanniae</i>	445	356.77	T	<i>Hylecoetus dermestoides</i> on <i>Quercus</i> sp.	Germany	H. Francke-Grosmann	OM501427	OM514768	OM631805	OM631630
<i>L. sylvestris</i>	<i>L. sylvestris</i>	23300	128833	P	<i>Picea abies</i>	Finland	Z.W. de Beer, P. Niemeiä	OM501454	OM514777	OM631827	-
<i>L. pseudoalbium</i>	<i>L. pseudoalbium</i>	40671	276.54	T	<i>Blastophagus piniperda</i> in <i>Pinus sylvestris</i>	Sweden	A. Mathiesen-Käärik	MN516723	MN516723	MN517755	OM631641
<i>L. raffai</i> <sup>#</sup>	<i>L. raffai</i>	34451	143468	T	<i>Dendroctonus valens</i>	California, USA	M.J. Wingfield	MT637219	MT637211	MT637206	-
<i>L. rhizoidum</i>	<i>L. rhizoidum</i>	22809	136512	T	<i>Hylastes ater</i> on <i>Pinus radiata</i>	Spain	P. Romón, X.D. Zhou	MN516724	MN516724	MN517748	OM631644
<i>L. tardum</i>	<i>L. tardum</i>	51789	144091	T	<i>Trypodendron domesticum</i> on <i>Fagus sylvatica</i>	Poland	R. Jankowiak	MH055529	-	MH055615	-
<i>L. vulnerum</i>	<i>L. vulnerum</i>	51794	144096	T	<i>Fagus sylvatica</i>	Poland	R. Jankowiak	MH055534	-	MH055620	-
<i>L. xiningense</i> <sup>#</sup>	<i>L. xiningense</i>	38891	136509	T	<i>Polygraphus poligraphus</i> in <i>Picea crassifolia</i>	China	M.L. Yin, X.D. Zhou	MN516732	MN516732	MN517752	OM631637
<b>Leptographium: L. piceiperdum complex</b>											
<i>G. aenigmatica</i>	<i>L. aenigmaticum</i>	2199	-	T	<i>Ips typographus japonicus</i> on <i>Picea jezoensis</i>	Japan	Y. Yamaoka	OM501416	OM514716	OM631791	OM631619
<i>G. europhoides</i>	<i>L. europhoides</i>	2811	115245		<i>Picea rubens</i>	New York, USA	T. Harrington	OM501426	OM514729	OM631804	OM631629
<i>G. laticis</i>	<i>L. laticis</i>	1913	120188		<i>Larix</i> sp.	Japan	Y. Yamaoka	-	DQ294393	-	-
<i>G. piceiperdum</i> <sup>†</sup>	<i>L. piceiperdum</i>	16768	138719		<i>Picea glauca</i>	Canada	K. Harrison	OM501435	OM514738	OM631812	OM631636
<i>G. pseudoeurophoides</i>	<i>L. pseudoeurophoides</i>	-	WIN(M)42		-	Canada	J. Reid	EU879136	-	-	-
<i>L. heilongjiangense</i>	<i>L. heilongjiangense</i>	44456	141702	T	<i>Ips typographus</i> on <i>Pinus koraiensis</i>	China	R. Chang	MH144098	-	MH124374	-
<i>L. zhangji</i>	<i>L. zhangji</i>	-	MUCL55162	T	<i>Ips subelongatus</i> on <i>Larix gmelinii</i>	China	X. Liu	KM236108	-	KM974275	-
<b>Leptographium: L. procerum complex</b>											
<i>L. bhutanense</i>	<i>L. bhutanense</i>	18649	122076	T	<i>Pinus wallichiana</i>	Bhutan	M.J. Wingfield	OM501418	OM514762	OM631794	-
<i>L. gracile</i>	<i>L. gracile</i>	12398	123623	T	<i>Pinus armandii</i>	China	X.D. Zhou	OM501430	OM514769	-	-

Table 1. (Continued).

Previous name	Current name	CMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	ITS	LSU	Tef1- $\alpha$	RPBII
<i>L. latens</i>	<i>L. latens</i>	12438	124023	T	<i>Picea koraiensis</i>	China	X.D. Zhou, Z.W. de Beer	HQ406845	-	HQ406869	-
<i>L. longiconidiophorum</i>	<i>L. longiconidiophorum</i>	2004	135624	T	<i>Hylastes</i> sp. on <i>Pinus densiflora</i>	Japan	M.J. Wingfield	KM491421	-	KM491471	-
<i>L. peucephyllum</i>	<i>L. peucephyllum</i>	2876	120191	T	<i>Picea</i> sp.	New York, USA	D. Bergdahl	-	-	-	-
<i>L. pini-densiflorae</i>	<i>L. pini-densiflorae</i>	5157	115261	T	<i>Pinus densiflora</i>	Japan	H. Masuya	OM501438	OM514774	OM631815	-
<i>L. procerum</i>	<i>L. procerum</i>	34542	138288	E	<i>Dendroctonus valens</i> on <i>Pinus resinosa</i>	Maine, USA	M.J. Wingfield	OM501442	OM514778	OM631816	OM631639
<i>L. profanum</i>	<i>L. profanum</i>	10552	120307	T	<i>Carya</i> sp.	Alabama, USA	L. Eckhardt	OM501443	OM514779	OM631817	OM631640
<i>L. sibiricum</i>	<i>L. sibiricum</i>	4481	115260	T	<i>Monochamus urussoni</i> on <i>Abies sibirica</i>	Russia	V.P. Vetrova	OM501451	OM514783	-	-
<i>L. sinense</i>	<i>L. sinense</i>	38171	316515	P	<i>Pinus elliotii</i>	China	M. Yin, R. Chang, X.D. Zhou	OM501452	OM514784	OM631825	OM631647
<i>L. sinoprocerum</i>	<i>L. sinoprocerum</i>	29990	MUCL46532	T	<i>Pinus tabulaeformis</i>	China	Q. Lu	OM501453	OM514785	OM631826	OM631648
<i>L. yichunense</i>	<i>L. yichunense</i>	44464	141705	T	<i>Ips typographus</i> on <i>Picea</i> sp.	China	R. Chang, S.F. Chen	MH144114	-	MH124390	-
<b>Leptographium: L. serpens complex</b>											
<i>G. alacris</i>	<i>L. alacris</i>	621	128830	T	<i>Pinus pinaster</i>	Portugal	M. de Fátima Moniz	OM501417	OM514717	OM631792	OM631620
<i>G. serpens</i>	<i>L. serpens</i>	305	141.36	T	<i>Pinus sylvestris</i>	Italy	G. Goidanich	OM501450	-	OM631824	OM631646
<i>L. castellanum</i>	<i>L. castellanum</i>	2320	128698	P	<i>Pinus occidentalis</i>	Dominican Republic	R. Webb	OM501420	OM514764	OM631798	OM631623
<i>L. gibbsii</i>	<i>L. gibbsii</i>	36371	-	T	<i>Hylastes opacus</i> on <i>Pinus sylvestris</i>	England, UK	J. Gibbs	OM501429	-	OM631807	OM631632
<i>L. rhodanense</i>	<i>L. rhodanense</i>	16438	138284	T	<i>Pinus sylvestris</i>	Switzerland	U. Heiniger	OM501448	-	OM631822	OM631645
<i>L. yamaokae</i>	<i>L. yamaokae</i>	4726	129732	T	<i>Pinus densiflora</i>	Japan	H. Masuya	-	-	OM631835	OM631655
<b>Leptographium: L. wageneri complex</b>											
<i>G. wageneri</i>	<i>L. wageneri</i> var. <i>ponderosum</i>	279	-		<i>Pinus</i> sp.	USA	T. Harrington	OM501458	OM514746	OM631831	OM631651
<i>L. douglasii</i>	<i>L. douglasii</i>	2076	-	P	<i>Pseudotsuga menziesii</i>	New Mexico, USA	M. Midke	OM501424	OM514766	OM631802	OM631627
<i>L. neomexicanum</i>	<i>L. neomexicanum</i>	2079	168.93	T	<i>Pinus ponderosa</i>	New Mexico, USA	T. Harrington, W. Livingston	AY553382	-	AY536176	-
<i>L. reconditum</i>	<i>L. reconditum</i>	15	116348		<i>Zea mays</i>	South Africa	W. Jooste	AF343690	-	AY536177	-
<i>L. wageneri</i> var. <i>pseudotsugae</i>	<i>L. wageneri</i> var. <i>pseudotsugae</i>	154	115246		<i>Pseudotsuga menziesii</i>	USA	T. Harrington	OM501459	OM514747	OM631832	OM631652
<i>L. wageneri</i> var. <i>wageneri</i>	<i>L. wageneri</i> var. <i>wageneri</i>	53	139665		<i>Pinus ponderosa</i>	California, USA	T. Harrington	OM501460	OM514788	OM631833	OM631653
<b>Leptographium: Group A</b>											
<i>L. pineti</i>	<i>L. pineti</i>	3837	115257		<i>Pinus</i> sp.	Indonesia	M.J. Wingfield	-	-	OM631814	OM631638
<i>L. ningerense</i>	<i>L. ningerense</i>	41786	139663	T	<i>Coccotrypes cyperi</i> on <i>Pinus kesiya</i>	China	S. Taerum	MG205674	-	MG205765	-
<b>Leptographium: Group B</b>											
<i>G. cainii</i>	<i>L. cainii</i>	24907	-		<i>Picea</i> sp.	Canada	C. Breuil	OM501389	OM514722	OM631797	OM631622
<b>Leptographium Incertae sedis (based on our data)</b>											
<i>G. huntii</i>	<i>G. huntii</i>	2868	118780		<i>Pinus strobus</i>	North Carolina, USA	V. Lackner	AY553394	-	DQ354938	-
<i>G. leptographioides</i>	<i>G. leptographioides</i>	481	144.59		<i>Quercus</i> sp.	New York, USA	R.W. Davidson	-	DQ294382	-	-

Table 1. (Continued).

Previous name	Current name	CIMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	GenBank Accession Numbers <sup>3</sup>			
								ITS	LSU	TEF1- $\alpha$	RPBII
<i>G. truncicola</i>	<i>G. truncicola</i>	-	-	-	<i>Dendroctonus</i> sp. on <i>Picea</i> sp.	USA	-	-	-	-	-
<i>L. albopini</i>	<i>L. albopini</i>	<sup>26</sup>	-	-	<i>Hylastes</i> sp. on <i>Pinus</i> sp.	USA	-	AF343695	-	-	-
<i>L. alethinum</i>	<i>L. alethinum</i>	<sup>3763</sup>	-	-	Galleries of <i>Hyllobius abietis</i> on log of <i>Pinus nigra</i> var. <i>maritima</i>	England, UK	A. Uzunovic	AY553391	-	AY536185	-
<i>L. calophylli</i>	<i>L. calophylli</i>	752	277.51	-	<i>Cryphalus</i> sp. on <i>Calophyllum</i> sp.	Mauritius	J.A. Stevenson	MH856855	MH868375	-	-
<i>L. microsporium</i>	<i>L. microsporium</i>	-	-	T	<i>Fagus</i> sp.	Mississippi, USA	R.W. Davidson	-	-	-	-
<i>L. obscurum</i>	<i>L. obscurum</i>	37429	125.39	-	<i>Pinus</i> sp.	USA	R.W. Davidson	-	-	-	-
<i>L. pityophilum</i>	<i>L. pityophilum</i>	2840	109706	-	<i>Pinus nigra</i>	Italy	S. Frisullo	OM501441	OM514776	-	-
<i>L. rostracylindricum</i>	<i>L. rostracylindricum</i>	-	-	-	<i>Quercus</i> sp.	Connecticut, USA	R.W. Davidson	-	-	-	-
<b>Leptographium &amp; Grosmanina incertae sedis (based on our data)</b>											
<i>L. guttulatum</i>	<i>L. guttulatum</i>	1310	120185	T	<i>Tomnicus piniperda</i> on <i>Pinus sylvestris</i>	England, UK	J. Gibbs	-	OM514770	-	-
<b>Lineage III</b>											
<i>G. crassivaginata</i>	<i>G. crassivaginata</i>	90	120178	-	-	-	T. Hinds	AF343673	-	-	-
<i>L. alneum</i> <sup>#</sup>	<i>L. alneum</i>	52076	144901	T	<i>Dryocoetes alni</i> infesting <i>Populus tremula</i>	Poland	K. Miskiewicz	MN900997	MN900997	MN901024	-
<i>L. piriforme</i>	<i>L. piriforme</i>	25381	UAMH10681	P	Beetle caught in a trap baited with coyote dung	Canada	M.D. Greif	OM501440	-	-	-
<b>Lineage VI</b>											
<i>L. verrucosum</i>	<i>L. verrucosum</i>	17160	112420	T	<i>Xyleborus dryographus</i>	Germany	H. Gebhardt	OM501456	OM514787	OM631830	OM631650
<b>Masuyamyces gen. nov.</b>											
<i>O. ambrosium</i>	<i>M. ambrosius</i>	1024	210.64	-	Wood of <i>Pinus sylvestris</i>	Netherlands	J.A. von Arx	OM501465	OM514793	OM631836	OM631656
<i>O. acarorum</i>	<i>M. acarorum</i>	41850	139748	T	<i>Orthotomicus angulatus</i> on <i>Pinus kesiya</i>	China	S. Taerum	MG205657	-	-	-
<i>O. botuliforme</i>	<i>M. botuliformis</i>	14493	-	-	<i>Cryphalus jeitollensis</i>	Japan	H. Masuya	OM501471	OM514799	OM631837	-
<i>O. jilinense</i>	<i>M. jilinensis</i>	40491	141894	T	<i>Ips typographus</i> on <i>Picea</i> sp.	China	X. D. Zhou	MH144094	-	MH124370	-
<i>O. lotiforme</i> <sup>#</sup>	<i>M. lotiformis</i>	-	MUCL55165	T	<i>Ips subelongatus</i> on <i>Pinus sylvestris</i> var. <i>mongolica</i>	China	X. Meng	MK748185	-	-	-
<i>O. massoniana</i>	<i>M. massoniana</i>	-	MUCL55179	T	<i>Monochamus</i> sp. on <i>Pinus</i> sp.	China	Q. Lu	KY094067	-	-	-
<i>O. pallidulum</i>	<i>M. pallidulus</i>	23278	128118	T	<i>Pinus sylvestris</i>	Russia	Z.W. de Beer, P. Niemelä	HM031510	-	-	-
<i>O. saponiodorum</i>	<i>M. saponiodorus</i>	28135	128302	T	<i>Pinus sylvestris</i>	Russia	R. Linnakoski	OM501512	OM514838	OM631838	OM631657
<b>Ophiostoma: O. clavatum complex</b>											
<i>O. ainoae</i>	<i>O. ainoae</i>	1037	205.83	T	<i>Picea abies</i>	Norway	H. Solheim	OM501463	OM514791	-	-
<i>O. brevipilosi</i>	<i>O. brevipilosi</i>	41873	139660	T	<i>Tomnicus brevipilosus</i> on <i>Pinus kesiya</i>	China	S. Taerum	MG205660	-	MG205732	-
<i>O. brunneociliatum</i>	<i>O. brunneociliatum</i>	5212	-	-	<i>Larix</i> sp.	Scotland, UK	T. Kirisits	KU184422	-	KU184379	-
<i>O. brunneolum</i>	<i>O. brunneolum</i>	23145	-	A	<i>Picea abies</i>	Russia	J. Anttinen, P. Niemelä	OM501472	OM514800	OM631843	OM631663
<i>O. clavatum</i>	<i>O. clavatum</i>	37983	141080	E	<i>Ips acuminatus</i> on <i>Pinus sylvestris</i>	Sweden	C. Villari	OM501477	OM514805	OM631848	-
<i>O. hongxingense</i> <sup>#</sup>	<i>O. hongxingense</i>	-	CFCC52695	T	<i>Ips subelongatus</i> on <i>Larix gmelinii</i>	China	Q. Lu	MK748194	-	MN896068	-
<i>O. japonicum</i>	<i>O. japonicum</i>	2202	YCC099	T	<i>Ips typographus japonicus</i> on <i>Picea jezoensis</i>	Japan	Y. Yamada	OM501492	-	OM631855	OM631673
<i>O. jiamusiensis</i>	<i>O. jiamusiensis</i>	40512	141893	T	<i>Ips typographus</i> on <i>Picea</i> sp.	China	X.D. Zhou	MH144064	-	MH124343	-

Table 1. (Continued).

Previous name	Current name	CMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	GenBank Accession Numbers <sup>3</sup>				
								ITS	LSU	TEF1- $\alpha$	RPBII	
<i>O. macroclavatum</i>	<i>O. macroclavatum</i>	23115	141081	T	<i>Pinus sylvestris</i>	Russia	Z.W. de Beer	HM031499	-	KU094765	-	
<i>O. penicillif</i> <sup>†</sup>	<i>O. peniculi</i>	-	C FCC52687	T	<i>Ips subelongatus</i> infesting <i>Larix gmelinii</i>	China	Q. Lu	MK748198	-	MN896063	-	
<i>O. poligraphi</i>	<i>O. poligraphi</i>	38899	136517	T	<i>Polygraphus poligraphus</i> on <i>Picea crassifolia</i>	China	M. Yin, S. Taerum, X.D. Zhou	OM501507	OM514832	OM631871	OM631688	
<i>O. pseudocatenulatum</i>	<i>O. pseudocatenulatum</i>	43103	141276	T	<i>Ips cembrae</i> on <i>Larix decidua</i>	Poland	R. Jankowiak	KU094686	-	KU094774	-	
<i>O. shangriilae</i>	<i>O. shangriilae</i>	38901	136519	T	<i>Ips shangrila</i> on <i>Picea purpurea</i>	China	M. Yin, S. Taerum, X.D. Zhou	OM501514	OM514840	OM631879	OM631695	
<i>O. songshui</i>	<i>O. songshui</i>	44473	141707	T	<i>Ips typographus</i> on <i>Picea</i> sp.	China	R. Chang, S.F. Chen	MH144065	-	MH124344	-	
<i>O. subelongati</i> <sup>†</sup>	<i>O. subelongati</i>	-	C FCC52693	T	<i>Ips subelongatus</i> infesting <i>Larix gmelinii</i>	China	Q. Lu	MK748200	-	MN896064	-	
<i>O. tapionis</i>	<i>O. tapionis</i>	23266	128122	P	<i>Picea abies</i>	Russia	Z.W. de Beer, P. Niemelä	OM501516	OM514842	OM631881	OM631697	
<i>Ophiostoma</i> sp. 3 ( <i>Hyalorhinoctadiella</i> sp. 2)	<i>Ophiostoma</i> sp. 3 ( <i>Hyalorhinoctadiella</i> sp. 2)	43851	UAMH10642		<i>Ips</i> sp.	Canada	S. Massoumi Alamouti	OM501524	OM514851	OM631888	-	
<i>Ophiostoma</i> sp. 4 ( <i>Hyalorhinoctadiella</i> sp. 1)	<i>Ophiostoma</i> sp. 4 ( <i>Hyalorhinoctadiella</i> sp. 1)	43848	UAMH10639		<i>Ips</i> sp.	Canada	S. Massoumi Alamouti	OM501525	OM514852	OM631889	OM631704	
<b>Ophiostoma: O. ips complex</b>												
<i>O. adjuncti</i>	<i>O. adjuncti</i>	1025	314.77	T	Stained sapwood in <i>Pinus ponderosa</i>	New Mexico, USA	R.W. Davidson	OM501462	OM514790	-	OM631658	
' <i>O. arborea</i> '	' <i>O. arborea</i> '	-	WIN(M)69-23		<i>Picea mariana</i>	Canada	A. Olchowecki, J. Reid	-	-	-	-	
<i>O. bicolor</i>	<i>O. bicolor</i>	23169	-		<i>Pinus sylvestris</i>	Russia	J. Ahtainen, P. Niemelä	OM501470	OM514798	OM631842	OM631662	
<i>O. columnare</i>	<i>O. columnare</i>	-	WIN(M)71-27		<i>Pinus banksiana</i>	Canada	A. Olchowecki, J. Reid	-	-	-	-	
<i>O. fuscum</i>	<i>O. fuscum</i>	23195	128124	P	<i>Pinus sylvestris</i>	Finland	Z.W. de Beer, P. Niemelä	OM501483	OM514810	-	OM631670	
<i>O. gilletteae</i> <sup>†</sup>	<i>O. gilletteae</i>	30681	143458	T	<i>Dendroctonus valens</i>	Washington, USA	N. Gillette	MT637227	-	-	-	
<i>O. guatemalensis</i>	<i>O. guatemalensis</i>	44221	-	T	<i>Pinus patula</i>	Guatemala	I. Barnes, J. Gamas	-	-	-	-	
<i>O. hyalothecium</i>	<i>O. hyalothecium</i>	-	ATCC28825		<i>Pinus contorta</i>	Wyoming, USA	R.W. Davidson	-	AF137284	-	-	
<i>Tuberculariella ips</i>	<i>O. ips</i> -like sp. 6	14175	435.34	T	<i>Ips</i> sp. on <i>Pinus</i> sp.	Minnesota, USA	J.G. Leach	OM501487	OM514813	OM631854	OM631672	
<i>O. ips</i> <sup>†</sup>	<i>O. ips</i>	19371	138721		<i>Pinus taeda</i>	Louisiana, USA	X.D. Zhou	OM501486	OM514812	OM631853	OM631671	
<i>O. manchongi</i> <sup>†</sup>	<i>O. manchongi</i>	41954	141906		<i>Uropodaidea</i> sp. in <i>Ips shangrila</i> gallery on <i>Picea purpurea</i>	China	S.J. Taerum	MH121662	-	-	-	
<i>O. montium</i>	<i>O. montium</i>	15419	-		<i>Pinus contorta</i>	Idaho, USA	B. Bentz	OM501498	OM514822	OM631861	OM631678	
<i>O. pseudobicolor</i> <sup>†</sup>	<i>O. pseudobicolor</i>	-	C FCC52683	T	<i>Ips subelongatus</i> in <i>Larix gmelinii</i>	China	Q. Lu	MK748188	-	-	-	
<i>O. pulvinisporum</i>	<i>O. pulvinisporum</i>	9022	118673	T	<i>Pinus pseudostrobus</i>	Mexico	X.D. Zhou	OM501509	OM514835	OM631874	OM631691	
<b>Ophiostoma: O. minus complex</b>												
' <i>O. album</i> '	' <i>O. album</i> '	-	MUCL55189	T	<i>Monochamus alternatus</i> gallery on <i>Pinus massoniana</i>	China	Q. Lu, Y.Y. Lun	KY094073	-	-	-	
<i>O. exiguum</i>	<i>O. exiguum</i>	-	-		<i>Pinus virginiana</i>	West Virginia, USA	G.G. Hedgcock	-	-	-	-	

Table 1. (Continued).

Previous name	Current name	CIMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	GenBank Accession Numbers <sup>3</sup>			
								ITS	LSU	TEF1- $\alpha$	RPBII
<i>O. kryptum</i>	<i>O. kryptum</i>	–	116190	T	Tetrapium on <i>Picea</i>	Austria	T. Kiritsis	AY305685	–	–	–
<i>O. minus</i>	<i>O. minus</i>	43873	UAMH4917		<i>Dendroctonus ponderosae</i> on <i>Pinus flexilis</i>	Canada	P. Muruyama	OM501497	OM514821	OM631860	OM631677
' <i>O. olgensis</i> '	' <i>O. olgensis</i> '	–	CXY1410	T	<i>Ips subelongatus</i> on <i>Larix olgensis</i>	China	Q. Lu	KU551303	–	KU551297	–
<i>O. minus</i> (in Europe)	<i>O. minus</i> (in Europe)	43346	–		<i>Pinus sylvestris</i>	Poland	T. Tomasz	–	–	–	–
<i>O. pseudominus</i>	<i>O. pseudominus</i>	43878	UAMH9721		<i>Pseudotsuga menziesii</i>	Canada	J. Reid, B. Reid	OM501508	OM514834	OM631873	OM631690
<i>O. pseudotsugae</i>	<i>O. pseudotsugae</i>	–	D48/3		–	Canada	H. Solheim	AY542501	–	–	–
<i>O. wuyingense</i>	<i>O. wuyingense</i>	44474	141706	T	<i>Ips typographus</i> on <i>Picea</i> sp.	China	R. Chang, S.F. Chen	MH144061	–	MH124340	–
<b>Ophiostoma: O. piceae complex</b>											
<i>O. arduennense</i> (= <i>O. distortum</i> )	<i>O. distortum</i>	40266	MUCL44866	T	<i>Fagus sylvatica</i>	Belgium	F.X. Cartier, T. Defrance	OM501468	OM514796	KU184376	–
<i>O. brunneum</i>	<i>O. brunneum</i>	1027	161.61	A	Standing dead <i>Abies</i> sp.	Colorado, USA	R.W. Davidson	OM501473	OM514801	OM631844	OM631664
<i>O. canum</i> ( <i>Pachnodium</i> )	<i>O. canum</i> ( <i>Pachnodium</i> )	5023	118668		<i>Tomiscus minor</i> on <i>Pinus sylvestris</i>	Austria	T. Kiritsis	OM501474	OM514802	OM631845	OM631665
<i>O. cupulatum</i>	<i>O. cupulatum</i>	37441	102358	T	<i>Pseudotsuga menziesii</i>	Washington, USA	T. Harrington	OM501479	OM514806	OM631849	OM631667
<i>O. distortum</i>	<i>O. distortum</i>	467	397.77	T	<i>Picea engelmannii</i>	Arizona, USA	R.W. Davidson	OM501481	OM514808	OM631850	OM631668
<i>O. flexuosum</i>	<i>O. flexuosum</i>	907	208.83	T	<i>Picea abies</i>	Norway	H. Solheim	OM501482	OM514809	OM631851	OM631669
<i>O. floccosum</i>	<i>O. floccosum</i>	34182	799.73	T	Wood	Sweden	A. Mathiesen-Käärk	KU184431	–	KU184388	–
<i>O. genhense</i> <sup>4</sup>	<i>O. genhense</i>	–	CFC52675	T	<i>Ips subelongatus</i> infesting <i>Larix gmelinii</i>	China	Q. Lu	MK748199	–	MN896074	–
<i>O. kunlunense</i> <sup>4</sup>	<i>O. kunlunense</i>	41927	141903	T	<i>Uropodoidea</i> sp. in gallery of <i>Ips shangrila</i> on <i>Picea purpurea</i>	China	S.J. Taerum	MH121648	–	MH124515	–
<i>O. micantis</i>	<i>O. micantis</i>	38903	136523	T	<i>Dendroctonus micans</i> on <i>Picea crassifolia</i>	China	M. Yin, S. Taerum, X.D. Zhou	OM501496	OM514820	OM631859	OM631676
<i>O. multisynnematum</i> <sup>4</sup>	<i>O. multisynnematum</i>	–	CFC52677		<i>Ips subelongatus</i> infesting <i>Larix gmelinii</i>	China	Q. Lu	MK748196	–	MN896071	–
<i>O. nikkoense</i>	<i>O. nikkoense</i>	17193	YCC430	T	<i>Polygraphus proximus</i>	Japan	Y. Yamaoka	OM501500	OM514824	OM631863	OM631679
<i>O. nitidi</i>	<i>O. nitidi</i>	38907	136525	T	<i>Picea crassifolia</i>	China	M. Yin, S. Taerum, X.D. Zhou	OM501501	OM514825	OM631864	OM631680
<i>O. perfectum</i>	<i>O. perfectum</i>	17153	600.85		Cat hairs	Germany	G.S. de Hoog	OM501506	OM514831	OM631868	OM631685
<i>O. peregrinum</i>	<i>O. peregrinum</i>	–	CIEFAP426	T	<i>Pinus radiata</i>	Argentina	A. de Errasti	MG345116	–	–	–
<i>O. piceae</i> <sup>4</sup>	<i>O. piceae</i>	–	UAMH11346		Pine saw timber	Canada	A. Uzunovic	MT633062	MT629745	OM631869	OM631686
<i>O. pityokteini</i> <sup>4</sup>	<i>O. pityokteinis</i>	52056	144879	T	<i>Pityokteines curvidens</i> infesting <i>Abies alba</i>	Poland	P. Majka	MH837046	–	MH837055	–
<i>O. qinghaiense</i>	<i>O. qinghaiense</i>	38902	136521	T	<i>Picea crassifolia</i>	China	M. Yin, S. Taerum, X.D. Zhou	OM501510	OM514836	OM631875	–
<i>O. rachisporum</i>	<i>O. rachisporum</i>	28021	–		<i>Picea abies</i>	Russia	R. Linnakoski	OM501511	OM514837	OM631877	OM631693
<i>O. rufum</i> <sup>4</sup>	<i>O. rufum</i>	52062	144871	T	<i>Ips cembrae</i> galleries on <i>Larix decidua</i>	Czech Republic	K. Lukášová	MH837040	–	KY568647	–
<i>O. setosum</i>	<i>O. setosum</i>	27833	AU160-38	T	<i>Tsuga</i> sp.	Canada	A. Uzunovic	OM501513	OM514839	OM631878	OM631694
<i>O. shanzenis</i> <sup>4</sup>	<i>O. shanzenis</i>	48329	MUCL46456	T	Phloem adjacent to <i>Dendroctonus valens</i> gallery in <i>Pinus tabulaeformis</i>	China	Q. Lu, C. Decock	MT637221	–	–	–
<i>O. sugadairense</i>	<i>O. sugadairense</i>	–	YCC589	T	<i>Polygraphus</i> sp. on <i>Larix</i> sp.	Japan	Y. Yamaoka	LC090227	–	AB934343	–

Table 1. (Continued).

Previous name	Current name	CMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	GenBank Accession Numbers <sup>3</sup>			
								ITS	LSU	TEF1- $\alpha$ RPBII	
<i>O. taphrotychi</i> <sup>#</sup>	<i>O. taphrotychi</i>	52045	144891	T	<i>Taphrotychus bicolor</i> infesting <i>Fagus sylvatica</i>	Poland	P. Biłanski	MH837052	–	MH837062	–
<i>O. typographi</i>	<i>O. typographi</i>	44483	141709	T	<i>Picea</i> sp.	China	R. Chang, S.F. Chen	MH144059	–	MH124337	–
<i>O. torulosum</i>	<i>O. torulosum</i>	10574	CTK106		<i>Fagus sylvatica</i>	Germany	T. Kirisits	OM501518	OM514844	OM631883	OM631699
<i>O. xinganense</i> <sup>#</sup>	<i>O. xinganense</i>	–	CFCC52679		<i>Ips subelongatus</i> infesting <i>Larix gmelinii</i>	China	Q. Lu	MK748186	–	MN896078	–
<b>Ophiostoma: O. pluriannulatum complex</b>											
<i>O. californicum</i>	<i>O. californicum</i>	143	796.73		<i>Prunus domestica</i>	California, USA	R.W. Davidson	KU756602	AF137280	–	–
<i>O. carpenteri</i>	<i>O. carpenteri</i>	44611	UAMH9696	P	<i>Trypodendron lineatum</i>	Oregon, USA	S. Carpenter	OM501475	OM514803	OM631846	–
<i>O. conicola</i>	<i>O. conicola</i>	2561	127.89	T	<i>Pinus cembroides</i>	Mexico	H. Butin	OM501478	–	–	–
<i>O. longiconidiatum</i>	<i>O. longiconidiatum</i>	14265	121350	A	<i>Faurea saligna</i>	South Africa	G. Kamgan Nkuekam	OM501494	OM514818	OM631857	–
<i>O. longirostellatum</i>	<i>O. longirostellatum</i>	–	134.51	T	<i>Quercus</i> sp.	Scotland, UK	B.K. Bakshi	–	AF155688	–	–
<i>O. multiannulatum</i>	<i>O. multiannulatum</i>	2567	357.77	T	<i>Pinus</i> sp.	North Carolina, USA	R.W. Davidson	OM501499	OM514823	OM631862	–
<i>O. novae-zelandiae</i>	<i>O. novae-zelandiae</i>	–	CIEFAP423	T	Dead fallen wood	New Zealand	–	KT362249	KT362226	–	–
<i>O. palustre</i>	<i>O. palustre</i>	44403	140596	T	<i>Barringtonia racemosa</i>	South Africa	J.A. Osorio	KU865593	–	–	–
<i>O. pluriannulatum</i>	<i>O. pluriannulatum</i>	–	MUCL18372		<i>Quercus</i> sp.	Oregon, USA	R.W. Davidson	AY934517	DQ294365	–	–
<i>O. populinum</i>	<i>O. populinum</i>	50149	212.67	T	<i>Populus tremuloides</i>	Colorado, USA	R.W. Davidson	–	OM514833	OM631872	OM631689
<i>O. retusi</i>	<i>O. retusi</i>	–	ATCC22324		<i>Populus</i> sp.	Colorado, USA	R.W. Davidson	–	L05783	–	–
<i>O. sparsiannulatum</i>	<i>O. sparsiannulatum</i>	17231	122815	T	<i>Pinus taeda</i>	Georgia, USA	L. Eckhardt	OM501515	OM514841	OM631880	OM631696
<i>O. subannulatum</i>	<i>O. subannulatum</i>	518	188.86		<i>Pinus</i> sp.	USA	W.H. Livingston, R.W. Davidson	AY934522	DQ294364	–	–
<b>Ophiostoma: O. ulmi complex</b>											
<i>O. allantosporum</i>	<i>O. allantosporum</i>	163	185.86		<i>Pinus resinosa</i>	Wisconsin, USA	M.J. Wingfield	OM501464	OM514792	OM631839	OM631659
<i>O. araucariae</i>	<i>O. araucariae</i>	40665	114.68	T	<i>Araucaria araucana</i>	Chile	H. Butin	OM501467	OM514795	–	–
<i>O. australiae</i>	<i>O. australiae</i>	6606	121025	T	<i>Acacia mearnsii</i>	Australia	M.J. Wingfield	EF408603	–	–	–
<i>O. bacillisporum</i>	<i>O. bacillisporum</i>	2579	MUCL45378	T	<i>Xyloterus domesticus</i> on <i>Fagus sylvatica</i>	Germany	F.X. Cartier	OM501469	OM514797	OM631841	OM631661
<i>O. borealis</i>	<i>O. borealis</i>	18966	123222	T	<i>Betula</i> logs	Norway	G. Kamgan Nkuekam, H. Solheim	EF408593	–	–	–
<i>O. cationianum</i>	<i>O. cationianum</i>	11535	263.35	A	<i>Pyrus communis</i>	Italy	G. Goidanich	AF198243	–	–	–
<i>O. dentifiliatum</i>	<i>O. dentifiliatum</i>	29493	124497	T	<i>Betula pendula</i>	Norway	R. Linnakoski	FJ804490	–	–	–
<i>O. himal-ulmi</i>	<i>O. himal-ulmi</i>	22729	ATCC36204		<i>Ulmus</i> sp.	India	H. Rebel	OM501484	OM514811	OM631852	–
<i>O. hylesini</i>	<i>O. hylesini</i>	51680	144296	T	<i>Hylesinus crenatus</i> on <i>Fraxinus excelsior</i>	Poland	P. Wieczorek	MH055636	MH055675	MH062835	–
<i>O. introcitrinum</i>	<i>O. introcitrinum</i>	–	UAMH9549	T	<i>Betula</i> sp.	Canada	A. Olchowicki	OM501485	–	–	–
<i>O. karelicum</i>	<i>O. karelicum</i>	23099	123219	T	<i>Scolytus</i> sp. on <i>Betula</i> sp.	Russia	Z.W. de Beer, P. Niemelä	OM501493	OM514817	OM631856	OM631674
<i>O. novo-ulmi</i> subsp. <i>americana</i>	<i>O. novo-ulmi</i> subsp. <i>americana</i>	43874	UAMH5030		<i>Ulmus americana</i>	–	–	–	OM514828	–	OM631683
<i>O. novo-ulmi</i> subsp. <i>novo-ulmi</i>	<i>O. novo-ulmi</i> subsp. <i>novo-ulmi</i>	–	H327		<i>Ulmus</i> sp.	Slovakia	H. Jammicky	OM501503	OM514827	OM631865	OM631682
<i>O. novo-ulmi</i> subsp. <i>novo-ulmi</i>	<i>O. novo-ulmi</i> subsp. <i>novo-ulmi</i>	43870	UAMH10443		<i>Ulmus</i> sp.	Iran	M. Rahju, K. Rahnama	OM501504	OM514829	OM631866	OM631684

Table 1. (Continued).

Previous name	Current name	CIMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	GenBank Accession Numbers <sup>3</sup>			
								ITS	LSU	TEF1- $\alpha$	RPBII
<i>O. patagonicum</i>	<i>O. patagonicum</i>	38089	CIEFAP431	T	<i>Nothofagus pumilio</i>	Argentina	A. de Errasti	OM501505	OM514830	OM631867	-
<i>O. pseudokarelicum</i>	<i>O. pseudokarelicum</i>	51704	144281	T	<i>Trypodendron domesticum</i> on <i>Alnus incana</i>	Norway	T. Aas	MH055659	MH055693	MH062859	-
<i>O. quercus</i> <sup>*</sup>	<i>O. quercus</i>	2465	117912		<i>Quercus robur</i>	France	M. Morelet	MT633064	MT629747	OM631876	OM631692
<i>O. signalum</i>	<i>O. signalum</i>	51689	144269	T	<i>Trypodendron signalum</i> on <i>Alnus incana</i>	Norway	G. Kvammen	MH055645	MH055682	MH062844	-
<i>O. tasmaniense</i>	<i>O. tasmaniense</i>	29088	127212	T	<i>Eucalyptus nitens</i> stumps	Australia	G. Kamgan Nkuekam	GU797211	-	GU797223	-
<i>O. tsotsi</i>	<i>O. tsotsi</i>	18134	123599	A	<i>Julbenardia globiflora</i>	Malawi	J. Roux	OM501520	OM514846	-	OM631701
<i>O. ulmi</i> <sup>*</sup>	<i>O. ulmi</i>	-	W9		<i>Ulmus</i> sp.	-	-	OM501521	OM514847	OM631885	OM631702
<i>O. undulatum</i>	<i>O. undulatum</i>	19396	127183		<i>Eucalyptus grandis</i>	Australia	M.J. Wingfield	-	OM514848	-	-
<i>O. villosum</i>	<i>O. villosum</i>	51694	144274	T	<i>Dryocoetes villosus</i> on <i>Quercus robur</i>	Norway	T. Aas, K.D. Hansen	MH055650	MH055685	MH062849	-
<b>Ophiostoma: Group H</b>											
<i>O. triangulosporum</i>	<i>O. triangulosporum</i>	1033	138.77	T	<i>Araucaria angustifolia</i>	Brazil	H. Butin	OM501519	OM514845	OM631884	OM631700
<b>Ophiostoma: Group I</b>											
<i>O. macrosporum</i> <sup>*</sup>	<i>O. macrosporum</i>	14176	367.53	T	<i>Pinus sylvestris</i>	Sweden	H. Francke-Grosmann	OM501495	OM514819	OM631858	OM631675
<i>O. tingens</i>	<i>O. tingens</i>	25530	366.53		<i>Xyleborus saxeseni</i> gallery in <i>Populus deltoides</i>	Sweden	H. Francke-Grosmann	-	EU177474	-	-
<i>Ophiostoma</i> sp. 1 ( <i>Ambrosiella</i> sp. 1)	<i>Ophiostoma</i> sp. 1 ( <i>Ambrosiella</i> sp. 1)	43827	UAMH10633		<i>Ips</i> sp.	Canada	S. Massoumi Alamouti	OM501522	OM514850	OM631887	OM631703
<i>Ophiostoma</i> sp. 2 ( <i>Ambrosiella</i> sp. 2)	<i>Ophiostoma</i> sp. 2 ( <i>Ambrosiella</i> sp. 2)	43828	UAMH10634		<i>Ips</i> sp.	Canada	S. Massoumi Alamouti	OM501523	-	-	-
<b>Ophiostoma: Group J</b>											
<i>O. piliferum</i> <sup>*</sup>	<i>O. piliferum</i>	-	-		-	-	-	MT633063	MT629746	OM631870	OM631687
<i>O. ponderosae</i>	<i>O. ponderosae</i>	37953	ATCC26665	T	Blue stain of <i>Pinus ponderosa</i>	Arizona, USA	R.W. Davidson	OM501554	OM514882	-	-
<b>Ophiostoma: Group K</b>											
<i>O. tetropii</i>	<i>O. tetropii</i>	4470	428.94		<i>Picea abies</i>	Austria	T. Kirişits	OM501517	OM514843	OM631882	OM631698
<b>Ophiostoma incertae sedis (based on our data)</b>											
<b>Lineage XVIII</b>											
<i>O. valdivianum</i>	<i>O. valdivianum</i>	449	454.83	T	<i>Nothofagus alpina</i>	Chile	H. Butin	-	OM514849	OM631886	-
<b>Lineage XX</b>											
<i>O. angusticollis</i>	<i>O. angusticollis</i>	152	-		<i>Pinus banksiana</i>	Wisconsin, USA	M.J. Wingfield	OM501466	OM514794	OM631840	OM631660
<i>O. denticulatum</i>	<i>O. denticulatum</i>	146	ATCC38087	T	<i>Gnathotrichus</i> sp. on <i>Pinus</i> sp.	Colorado, USA	R.W. Davidson	OM501480	OM514807	-	-
<i>O. sejunctum</i>	<i>O. sejunctum</i>	-	Ophi 1A	T	<i>Tomicus</i> sp. on <i>Pinus</i> sp.	Spain	M.R. Boreal	AY934519	-	-	-
<b>Lineage XXIII</b>											
<i>O. noisomeae</i>	<i>O. noisomeae</i>	40326	-	T	<i>Rapanea melanophloeos</i>	South Africa	T. Musvuugwa	OM501502	OM514826	-	OM631681
<b>Paleoambrosia</b>											
<i>P. entomophila</i>	<i>P. entomophila</i>	-	No. B-F-7	T	<i>Palaeotylus femoralis</i> in burmese amber	Myanmar	G.O. Poinar, F.E. Vega	-	-	-	-

Previous name	Current name	CMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	GenBank Accession Numbers <sup>3</sup>			
								ITS	LSU	TEF1- $\alpha$	RPBII
<b>Raffaelea</b>											
<i>R. albimanens</i> <sup>*</sup>	<i>R. albimanens</i>	25532	271.70	T	<i>Platypus extermedentatus</i> in <i>Ficus sycomorua</i>	South Africa	D.B. Scott	MT633066	MT629749	OM631890	OM631705
<i>R. ambrosiae</i> <sup>*</sup>	<i>R. ambrosiae</i>	25533	185.64	T	<i>Platypus cylindrus</i> tunnel in <i>Quercus</i> sp.	England, UK	J.M. Bakeer	MT633067	MT629751	OM631891	OM631706
<i>R. arxii</i>	<i>R. arxii</i>	25534	273.70	T	<i>Xyleborus forquatus</i> on <i>Cussonia</i> sp.	South Africa	D.B. Scott	-	MT629754	OM631892	OM631708
<i>R. borbonica</i> <sup>#</sup>	<i>R. borbonica</i>	51553	PPR127953	T	<i>Leucaena leucocephala</i>	Réunion, France	M.J. Wingfield, P.W. Crous	MT633059	MT629742	-	-
<i>R. campbelliorum</i>	<i>R. campbelliorum</i>	44800	139943	T	<i>Xyleborus glabratus</i> on <i>Persea palustris</i>	Florida, USA	A.S. Campbell	-	KR018414	-	-
<i>R. canadensis</i>	<i>R. canadensis</i>	25536	168.66	T	<i>Platypus wilsonii</i> in <i>Pseudotsuga menziesii</i>	Canada	A. Funk	GQ225699	MT629755	-	-
<i>R. canadensis</i> (=A. sulcati)	<i>R. canadensis</i>	25528	805.70	T	<i>Gmnaothrichus sulcatus</i> (mycangium) on <i>Pseudotsuga menziesii</i>	Canada	A. Funk	-	EU177459	-	-
<i>R. crossotarsi</i>	<i>R. crossotarsi</i>	44793	141675	T	Mycangium extract of <i>Crossotarsus emancipatus</i> in <i>Lithocarpus</i> sp.	Taiwan	J. Hulcr, A. Black, D.R. Simmons	KX267138	MT629756	OM631893	OM631709
<i>R. cyclohipidii</i>	<i>R. cyclohipidii</i>	44790	141676	T	<i>Cyclohipidion</i> sp. on <i>Lithocarpus</i> sp.	Taiwan	J. Hulcr, A. Black, D.R. Simmons	MT633069	MT629757	-	OM631710
<i>R. ellipticospora</i>	<i>R. ellipticospora</i>	38056	121569	T	<i>Xyleborus glabratus</i> on <i>Persea</i> sp.	South Carolina, USA	S. Fraedrich	MT633070	MT629758	OM631894	-
<i>R. fusca</i>	<i>R. fusca</i>	38798	121570	T	<i>Xyleborus glabratus</i> on <i>Persea</i> sp.	South Carolina, USA	S. Fraedrich	-	EU177449	-	-
<i>R. gnathotrichi</i>	<i>R. gnathotrichi</i>	25523	379.68	T	<i>Gnathotrichus retusus</i> on <i>Picea engelmannii</i>	Colorado, USA	L.R. Batra	-	EU177460	-	-
<i>R. promiscua</i> <sup>#</sup>	<i>R. promiscua</i>	55899	147173	T	<i>Xyleborinus saxesenii</i>	South Africa	W.J. Nel	MW028176	-	-	-
<i>R. rapaneae</i>	<i>R. rapaneae</i>	40357	140084	T	<i>Platypodinae</i> sp. on <i>Rapanea melanophloeos</i>	South Africa	T. Musvuugwa	KT192596	KT182930	-	-
<i>R. santoroii</i>	<i>R. santoroii</i>	25539	399.67	T	<i>Platypus</i> sp. bore hole	Argentina	J. Wright	MT633075	MT629765	-	-
<i>R. scolytoidis</i>	<i>R. scolytoidis</i>	23001	CCF3566	A	<i>Scolytodes</i> sp. on <i>Cecropia</i> sp.	Costa Rica	M. Kolarik	AM267264	-	-	-
<i>R. seticollis</i>	<i>R. seticollis</i>	1031	634.66	T	<i>Tsuga canadensis</i>	New York, USA	R.W. Davidson	MT633076	MT629766	OM631895	OM631711
<i>R. subalba</i>	<i>R. subalba</i>	38797	121568	T	<i>Xyleborus</i> sp. on <i>Persea</i> sp.	South Carolina, USA	S. Fraedrich	-	MT629767	-	OM631712
<i>R. subfusca</i>	<i>R. subfusca</i>	38055	121571	T	<i>Xyleborus glabratus</i>	South Carolina, USA	S. Fraedrich	-	EU177450	-	-
<i>R. sulcati</i>	<i>R. sulcati</i>	25540	806.70	T	<i>Gnathotrichus sulcatus</i> mycangium in <i>Pseudotsuga menziesii</i>	Canada	A. Funk	-	EU177462	-	-
<i>R. tritirachium</i>	<i>R. tritirachium</i>	25541	726.69	T	<i>Monarthrum mali</i> tunnel in <i>Quercus</i> sp.	Pennsylvania, USA	D.B. Scott	-	EU177464	-	-
<i>R. xyleborini</i>	<i>R. xyleborini</i>	45859	Hulcr6099	T	<i>Xyleborinus andrewesii</i>	Florida, USA	C. Bateman	MT633078	MT629769	-	-
<i>Raffaelea</i> sp. A (PL1001)	<i>Raffaelea</i> sp. A (PL1001)	38062	-	-	<i>Persea</i> sp.	California, USA	A. Eskalen	-	KJ909293	-	-
<b>Raffaelea incertae sedis (based on our data)</b>											
<i>R. deltoideospora</i>	<i>R. deltoideospora</i>	-	WIN(M)41	-	<i>Pinus</i> sp.	Canada	J. Reid	EU879121	KT182932	-	-
<b>Lineage X</b>											
<i>R. vaginata</i>	<i>R. vaginata</i>	40365	140086	T	<i>Lanurgus</i> sp. on <i>Olea capensis</i>	South Africa	T. Musvuugwa	KT192602	-	-	-
<b>Sporothrix: S. candida complex</b>											
<i>S. aemulophila</i>	<i>S. aemulophila</i>	40381	140087	T	<i>Rapanea melanophloeos</i>	South Africa	T. Musvuugwa	OM501527	OM514854	OM631897	-
<i>S. cabralii</i>	<i>S. cabralii</i>	38098	CIEFAP456	T	<i>Nothofagus pumilio</i>	Argentina	A. de Errasti	OM501533	OM514861	OM631903	OM631716
<i>S. candida</i>	<i>S. candida</i>	26484	129713	T	<i>Eucalyptus cloeziana</i>	South Africa	G. Kamgan Nkuekam	-	OM514862	OM631904	OM631717
<i>S. itsvo</i>	<i>S. itsvo</i>	40370	141063	T	<i>Rapanea melanophloeos</i>	South Africa	T. Musvuugwa	KX590840	-	-	-



Table 1. (Continued).

Previous name	Current name	CMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	ITS	LSU	TEF1- $\alpha$	RPBII	
<i>S. oleae</i> <sup>#</sup>	<i>S. oleae</i>	40362	142082	T	<i>Olea capensis</i> ssp. <i>macrocarpa</i> wound	South Africa	T. Musvuugwa	MN298851	-	-	-	
<i>S. rapaneae</i>	<i>S. rapaneae</i>	40369	141060	T	<i>Rapanea melanophloeos</i>	South Africa	T. Musvuugwa	OM501558	OM514885	OM631926	OM631735	
<b>Sporothrix: S. inflata complex</b>												
<i>S. dentifunda</i>	<i>S. dentifunda</i>	13016	115790	T	<i>Quercus</i> wood	Hungary	C. Delatour	OM501535	OM514865	OM631907	OM631718	
<i>S. dimorphospora</i>	<i>S. dimorphospora</i>	12529	553.74	T	Soil	Canada	R.A.A. Morall	OM501536	OM514866	OM631908	OM631719	
<i>S. guttuliformis</i>	<i>S. guttuliformis</i>	17167	437.76	T	Soil	Malaysia	T. Furukawa	OM501542	OM514873	OM631915	OM631725	
<i>S. inflata</i>	<i>S. inflata</i>	12527	239.68	T	Wheat field soil	Canada	W. Gams	OM501544	-	OM631917	OM631727	
<i>Spumatoria longicollis</i>	<i>S. longicollis</i>	49345	141464	E	Dung	Netherlands	J. vd Lee	-	OM514895	OM631933	-	
<b>Sporothrix: S. stenoceras &amp; S. gossypina complexes</b>												
<i>S. abietina</i> <sup>*</sup>	<i>S. abietina</i>	22310	125.89	T	<i>Pseudohylesinus</i> gallery on <i>Abies vejarii</i>	Mexico	J.G. Marmolejo	OM501526	OM514853	OM631896	OM631713	
<i>S. africana</i>	<i>S. africana</i>	823	116571	T	<i>Protea gaguedi</i>	South Africa	M.J. Wingfield	OM501528	OM514855	OM631898	OM631714	
<i>S. aurorae</i>	<i>S. aurorae</i>	19362	118837	T	<i>Hylastes angustatus</i> on <i>Pinus elliotii</i>	South Africa	X.D. Zhou	-	OM514857	OM631900	-	
<i>S. cantabrigiensis</i>	<i>S. cantabrigiensis</i>	39766	136529	T	<i>Hylastes attenuatus</i> on <i>Pinus sylvestris</i>	Spain	P. Romón	KF951554	-	-	-	
<i>S. cracoviensis</i> <sup>#</sup>	<i>S. cracoviensis</i>	-	147942	T	Adult of <i>Trypodendron domesticum</i> beetle on <i>Fagus sylvaticum</i>	Poland	R. Jankowiak	MW768964	-	-	-	
<i>S. eucastaneae</i>	<i>S. eucastaneae</i>	1124	424.77	T	Canker on <i>Castanea dentata</i>	North Carolina, USA	R.W. Davidson	OM501539	OM514868	OM631910	OM631720	
<i>S. euskadiensis</i>	<i>S. euskadiensis</i>	27318	122138	T	<i>Hylurgops palliatus</i> on <i>Pinus radiata</i>	Spain	X.D. Zhou	DQ674369	-	-	-	
<i>S. fraxini</i> <sup>#</sup>	<i>S. fraxini</i>	-	147936	T	Gallery of <i>Hylesinus varius</i> on <i>Fraxinus excelsior</i>	Poland	R. Jankowiak	MH283150	-	-	-	
<i>S. fusiformis</i>	<i>S. fusiformis</i>	9968	112912	T	<i>Populus nigra</i>	Azerbaijan	D. Aghayeva	-	OM514870	OM631912	OM631722	
<i>S. gossypina</i>	<i>S. gossypina</i>	1116	ATCC18999	T	<i>Pinus ponderosa</i>	New Mexico, USA	R.W. Davidson	-	-	OM631914	OM631724	
<i>S. villosa</i> <sup>#</sup>	<i>S. villosa</i>	-	SNM188	T	<i>Pinus thunbergii</i>	China	R. Chang	MW989428	-	MZ853078	-	
<i>S. lunata</i>	<i>S. lunata</i>	10563	112927	T	<i>Carpinus betulus</i>	Austria	T. Kiritsis	OM501545	-	OM631918	OM631728	
<i>S. narcissi</i>	<i>S. narcissi</i>	22311	138.50	T	<i>Narcissus</i> sp.	Netherlands	D.P. Limber	OM501548	-	OM631920	-	
<i>S. nsini</i>	<i>S. nsini</i>	28602	143281	T	<i>Protea caffra</i>	South Africa	F. Roets	EU660458	-	-	-	
<i>S. prolifera</i>	<i>S. prolifera</i>	37435	251.88	T	<i>Quercus robur</i>	Poland	T. Kowalski	OM501555	-	OM631924	OM631732	
<i>S. protearum</i>	<i>S. protearum</i>	1107	116654	T	<i>Protea caffra</i>	South Africa	M.J. Wingfield	OM501557	OM514884	OM631925	OM631734	
<i>S. resoviensis</i> <sup>#</sup>	<i>S. resoviensis</i>	-	147927	T	Wound on <i>Betula pendula</i>	Poland	R. Jankowiak	MH740962	-	-	-	
<i>S. rossii</i>	<i>S. rossii</i>	1118	116.78	T	<i>Dendroctonus adjunctus</i> gallery on <i>Pinus ponderosa</i>	New Mexico, USA	R.W. Davidson	OM501559	OM514886	OM631927	OM631736	
<i>S. splendens</i> <sup>*</sup>	<i>S. splendens</i>	23050	138722	T	<i>Oodiniichus</i> sp. on <i>Protea repens</i>	South Africa	F. Roets	OM501561	OM514888	OM631929	OM631738	
<i>S. stenoceras</i>	<i>S. stenoceras</i>	3202	237.32	T	Pine pulp	Norway	H. Robak	AF484462	DQ294350	-	-	
<i>S. uta</i>	<i>S. uta</i>	40316	141069	P	<i>Rapanea melanophloeos</i>	South Africa	T. Musvuugwa	OM501565	OM514892	OM631930	OM631739	
<i>S. varicibata</i>	<i>S. varicibata</i>	23051	121961	T	<i>Trichouropoda</i> sp. from <i>Protea repens</i>	South Africa	F. Roets	OM501566	OM514893	OM631931	OM631740	
<i>S. zambiensis</i>	<i>S. zambiensis</i>	29077	124914	T	<i>Protea caffra</i>	Zambia	F. Roets	OM501567	OM514894	OM631932	OM631741	
<b>Sporothrix: S. pallida complex</b>												
<i>S. albicans</i> (syn <i>S. pallida</i> )	<i>S. albicans</i> (syn <i>S. pallida</i> )	17203	302.73	T	Soil	England, UK	S.B. Saksena	OM501529	OM514856	OM631899	OM631715	

Table 1. (Continued).

Previous name	Current name	CMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	ITS	LSU	TEF1- $\alpha$	RPBII	
<i>S. chilensis</i>	<i>S. chilensis</i>	49343	139890	T	Soil	Chile	R. Cruz Choappa	-	OM514863	OM631905	-	
<i>S. gemella</i>	<i>S. gemella</i>	23057	121959	T	<i>Tarsonemus</i> sp. on <i>Protea caffra</i>	South Africa	F. Roets	DQ821560	DQ821531	-	-	
<i>S. humicola</i>	<i>S. humicola</i>	7618	118129	T	Soil	South Africa	H.F. Vismer	OM501543	-	OM631916	OM631726	
<i>S. mexicana</i>	<i>S. mexicana</i>	29129	120341	T	Soil	Mexico	A. Espinosa	OM501547	OM514875	OM631919	-	
<i>S. pallida</i>	<i>S. pallida</i>	17209	131.56	T	<i>Stemonitis fusca</i>	Japan	K. Tubaki	OM501550	OM514878	OM631921	OM631729	
<i>S. palmiculminata</i>	<i>S. palmiculminata</i>	20677	119590	T	<i>Protea repens</i>	South Africa	F. Roets	OM501551	OM514879	OM631922	OM631730	
<i>S. protea-sedis</i>	<i>S. protea-sedis</i>	29074	124911	P	<i>Protea caffra</i>	Zambia	F. Roets	OM501556	OM514883	-	OM631733	
<i>S. stylites</i>	<i>S. stylites</i>	14543	118848	T	Pine utility poles	South Africa	E.M. de Meyer	OM501563	OM514890	-	-	
<b>Sporothrix: Pathogenic clade</b>												
<i>S. brasiliensis</i>	<i>S. brasiliensis</i>	29127	120339	T	Human skin	Brazil	M.D.S. Lazera	OM501531	OM514859	OM631901	-	
<i>S. globosa</i>	<i>S. globosa</i>	29128	120340	T	Human face	Spain	C. Rubio	OM501541	OM514872	OM631913	OM631723	
<i>S. luriei</i>	<i>S. luriei</i>	17210	937.72	T	Human skin	South Africa	L. Lurie	OM501546	-	-	-	
<i>S. schenckii</i>	<i>S. schenckii</i>	38850	138723	T	Clinical isolate	South Africa	H.F. Vismer	OM501560	OM514887	OM631928	OM631737	
<b>Sporothrix: Group D</b>												
<i>S. cavum</i> <sup>#</sup>	<i>S. cavum</i>	-	147943	T	Cavity of <i>Dendrocopos major</i> on <i>Salix fragilis</i>	Poland	R. Jankowiak	MF782813	MF782813	-	-	
<i>S. polyporicola</i>	<i>S. polyporicola</i>	5461	669.88	T	<i>Fomitopsis pinicola</i>	Sweden	S. Ryman	OM501553	OM514881	-	-	
<b>Sporothrix: Group E</b>												
<i>S. phasma</i>	<i>S. phasma</i>	20676	119722	T	<i>Protea laurifolia</i>	South Africa	F. Roets	OM501552	OM514880	OM631923	OM631731	
<b>Sporothrix: Group F</b>												
<i>S. braganina</i>	<i>S. braganina</i>	17149	474.91	T	Soil	Brazil	W. Gams	OM501530	OM514858	-	-	
<i>S. curviconia</i>	<i>S. curviconia</i>	17164	959.73	T	<i>Terminalia ivorensis</i>	Ivory Coast	J. Devois	OM501534	OM514864	OM631906	-	
<i>S. epigloea</i>	<i>S. epigloea</i>	22308	573.63	T	<i>Tremella fuciformis</i>	Argentina	R. T. Guerrero	KX590817	KX590854	-	-	
<i>S. eucalyptigena</i>	<i>S. eucalyptigena</i>	45431	139899	T	<i>Eucalyptus</i> sp.	Australia	P.A. Barber	OM501538	-	OM631909	-	
<i>S. nebularis</i>	<i>S. nebularis</i>	27319	122135	T	<i>Hylastes attenuatus</i> on <i>Pinus radiata</i>	Spain	P. Romón	KX590823	KX590862	-	-	
<i>S. nigrograna</i>	<i>S. nigrograna</i>	14487	MAFF410943	T	<i>Pinus densiflora</i>	Japan	H. Masuya	OM501549	OM514877	-	-	
<i>S. smargaliso</i>	<i>S. smargaliso</i>	50502	143341	T	<i>Protea gaguedi</i>	South Africa	N.P. Ngubane	MF103773	-	-	-	
<i>S. thermara</i>	<i>S. thermara</i>	38930	139747	T	<i>Cyrtogenius africanus</i> on <i>Euphorbia ingens</i>	South Africa	J.A. van der Linde	OM501564	OM514891	-	-	
<i>S. zhejiangensis</i>	<i>S. zhejiangensis</i>	-	MUCL55183	T	<i>Monochamus</i> sp. on <i>Pinus</i> sp.	China	Q. Lu, Y.Y. Lun	KY094071	-	-	-	
<b>Sporothrix: Group G</b>												
<i>S. dombeyi</i>	<i>S. dombeyi</i>	1023	455.83	T	<i>Nothofagus</i> sp.	Chile	H. Butin	OM501537	OM514867	-	-	
<b>Sporothrix incertae sedis (based on our data)</b>												
<b>Lineage XVI</b>												
<i>S. fumea</i>	<i>S. fumea</i>	26813	129712	T	<i>Phoracantha</i> sp. galleries on <i>Eucalyptus</i>	South Africa	C. Perez	OM501540	OM514869	OM631911	OM631721	
<b>Lineage XIX</b>												
<i>S. brunneoviolacea</i>	<i>S. brunneoviolacea</i>	37442	124560	P	Soil	Spain	C. Silvera	OM501532	OM514860	OM631902	-	
<b>Sporothrix incertae sedis (based on published data)</b>												
<i>S. cryptarctum</i> <sup>#</sup>	<i>S. cryptarctum</i>	-	147934	T	Adult of <i>Cryptarctia undata</i>	Poland	R. Jankowiak	MW768966	-	-	-	
<i>S. hypoxylif</i> <sup>#</sup>	<i>S. hypoxylif</i>	47441	141569	T	<i>Hypoxylon petrinae</i> on <i>Fraxinus</i> wood	Netherlands	E. Osieck & W.J. Nel	MT637058	MW012948	-	-	

Table 1. (Continued).

Previous name	Current name	CMW <sup>1</sup>	CBS or other <sup>1</sup>	Type <sup>2</sup>	Isolated from	Country	Collector	ITS	LSU	TEF1- $\alpha$	RPBII	
<i>S. undulata</i> <sup>#</sup>	<i>S. undulata</i>	-	147929	T	Adult of <i>Epuraea guttata</i>	Poland	R. Jankowiak	MH740976	-	-	-	
<b>Ophiostomatales insertae sedis (based on published data)</b>												
<i>L. antibioticum</i>	<i>L. antibioticum</i>	2777	DAOM84338	T	<i>Pinus taeda</i>	Georgia, USA	S. Alexander	AF343677	-	-	-	
<i>L. brachiatum</i>	<i>L. brachiatum</i>	2855	C388	T	<i>Picea rubens</i>	New York, USA	S. Alexander	AF343676	-	-	-	
<i>L. elegans</i>	<i>L. elegans</i>	2245	115241		<i>Chamaecyparis / Hinoke</i>	Taiwan	M.J. Wingfield	AF343675	-	-	-	
<i>O. crenulatum</i>	<i>O. crenulatum</i>	-	WIN(M)70-17	T	<i>Pinus banksiana</i>	Canada	J. Reid	-	AF135589	-	-	
<i>O. fasciatum</i>	<i>O. fasciatum</i>	-	UM56		<i>Pseudotsuga menziesii</i>	Canada	A. Olchoweki	EU913720	EU913680	-	-	
<i>O. brevisculum</i>	<i>O. brevisculum</i>	-	YCC522		Single ascospore isolate from YCC-494	Japan	Y. Yamaoka	AB200423	-	-	-	
<i>O. ssiiori</i>	<i>O. ssiiori</i>	-	MAFF410973	T	<i>Polygraphus ssiiori</i> on <i>Prunus</i> sp.	Japan	H. Masuya	AB096209	-	-	-	
<i>O. subalpinum</i>	<i>O. subalpinum</i>	-	YCC408		<i>Cryphalus</i> sp. on <i>Abies</i> sp.	Japan	Y. Yamaoka	AB200424	-	LC090750	-	
<i>O. pseudonigrum</i>	<i>O. pseudonigrum</i>	-	WIN(M)71-13		<i>Picea mariana</i>	Canada	J. Reid	-	AF135577	-	-	
<i>O. pehuenuinum</i>	<i>O. pehuenuinum</i>	-	142995	T	<i>Araucaria araucana</i>	Chile	V. Sepúlveda	MF576438	-	MF576446	-	
<i>O. tremulo-aureum</i>	<i>O. tremulo-aureum</i>	-	361.65		Black canker on <i>Populus tremuloides</i>	Colorado, USA	R.W. Davidson	-	AF135573	-	-	

ATCC = American Type Culture Collection, Maryland, USA; CBS = the culture collection of Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CFCC = China Forestry Culture Collection Center, Research Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing, China; CIEFAP = the culture collection of the Centro de Investigación y Extensión Forestal Andino Patagónico, Argentina; CMW = the culture collection of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa; CTK = the culture collection of the Institute of Forest Entomology, Forest Pathology and Forest Protection, Department of Forest and Soil Sciences, University of Natural Resources and Applied Life Sciences, Vienna, Austria; CXY = the culture collection of the Chinese Academy of Forestry, China; DAOM = Canadian National Mycological Herbarium, Ottawa, Canada; KACC = Korean Agricultural Culture Collection, Suwon, Korea; KUC = Korea University Culture Collection, Seoul, Korea; MAFF = the culture collection of National Institute of Agrobiological Resources, Japan; MUCL = BCCM/MUCL Agro-food & Environmental Fungal Collection, Université catholique de Louvain, Belgium; PPRI = National Collection of Fungi, Pretoria, South Africa; RWD = the private collection of R.W. Davidson; SNM = the microbial culture collection of Shandong Normal University, Jinan, Shandong, China; TRTC = Royal Ontario Museum Fungarium, Toronto, Canada; UAMH = University of Alberta Mold Herbarium and Culture Collection, Edmonton, Canada; VPRI = Victorian Plant Pathology Herbarium, Victoria, Australia; WIN(M) = University of Manitoba, Microbiology and Botany (J. Reid's personal collection); YCC = the private collection of Y. Yamaoka.

<sup>2</sup> T = ex-type, E = ex-epitype, P = ex-paratype, L = ex-lectotype; A = authentic isolate, used in the original study.

<sup>1</sup> Genome data used in this study.

<sup>#</sup> Species published after 2018, thus not included in the current analyses.

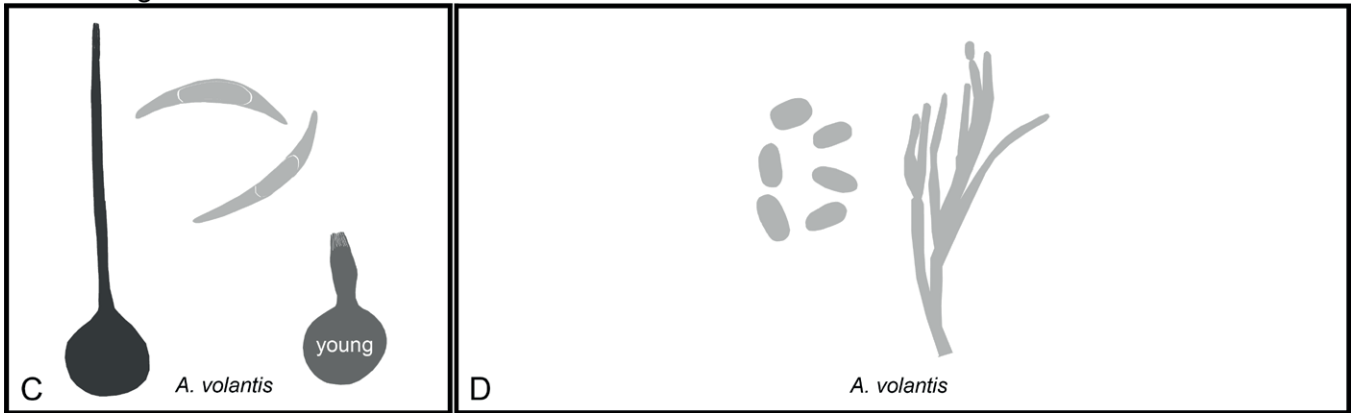
<sup>^</sup> CMW culture replaced with a different fungus.

<sup>3</sup> Sequences with accession numbers preceded with "OM" were generated in the current study.

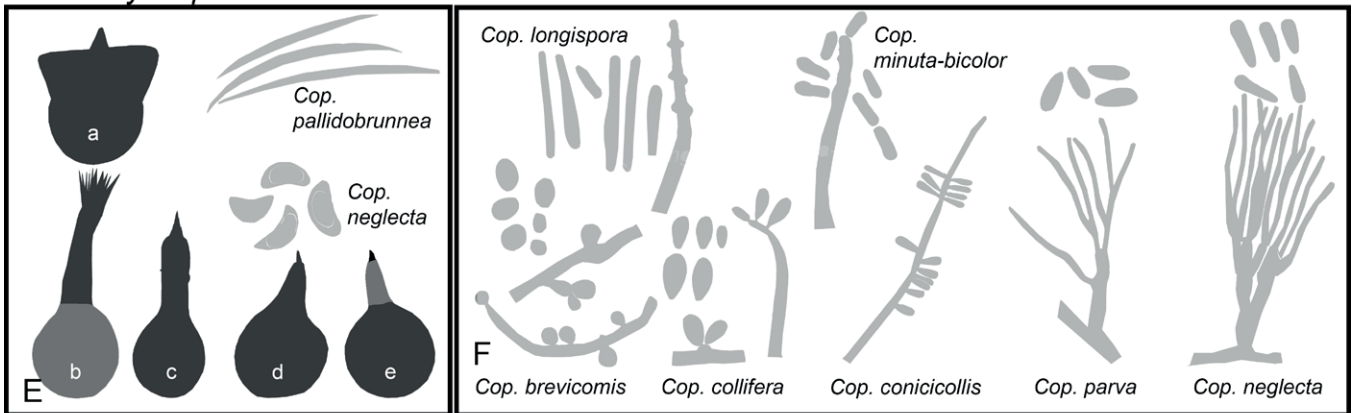
*Afroraffaelea*



*Aureovirgo*



*Ceratocystiopsis*



*Chrysosphaeria*



Fig. 6. Genera of the *Ophiostomatales* redrawn from published images with sexual morphs (if known) on the left and asexual morphs on the right. A, B. *Afroraffaelea*. C, D. *Aureovirgo*. E, F. *Ceratocystiopsis* (a. *Cop. collifera*; b. *Cop. ochracea*; c. *Cop. manitobensis*; d. *Cop. concentrica*; e. *Cop. rollhanseni*). G, H. *Chrysosphaeria*. (Pale grey shading reflects hyaline to subhyaline colouration, medium-tone grey brown to dark brown and dark grey reflects fuscous black to dark black colouration).

*Notes:* In their revision of the genus *Ceratocystis*, Upadhyay & Kendrick (1975) erected *Ceratocystiopsis* for species with falcate ascospores and a *Hyalorhinochlaetia* asexual morph. Hausner *et al.* (1993a) reduced *Ceratocystiopsis* to synonymy with *Ophiostoma* based on rDNA sequences, but Zipfel *et al.* (2006) included additional taxa in their study and reinstated the genus that is typified by *Ceratocystiopsis minuta*. Species in this genus have elongated sickle-shaped (falcate) ascospores that are sheathed, produced in very short necked ascomata, characters not seen in any other genus in the *Ophiostomatales* (Upadhyay & Kendrick 1975, Zipfel *et al.* 2006, De Beer & Wingfield 2013). Species of *Ceratocystiopsis* are found in the galleries of conifer-infesting bark beetles (*Dendroctonus* species in North America or *Ips* species in Japan and Europe) in the Northern Hemisphere (Plattner *et al.* 2009).

*Ceratocystiopsis* spp. formed a well-supported monophyletic clade in all our phylogenies, supporting the decision of Zipfel *et al.* (2006) to reinstate the genus. Our data also supported the placement of *Cop. neglecta* (previously *Ophiostoma neglectum*) in *Ceratocystiopsis*, as shown by De Beer & Wingfield (2013).

## **Chrysosphaeria**

***Chrysosphaeria*** W.J. Nel *et al.*, Mycologia 113: 1206. 2021. MycoBank MB 837564. Fig. 6G, H.

*Etymology:* 'From Latin chryso-, golden, and -sphaera, sphere or orb, referring to the light colour of the ascoma bases in the type species' (Nel *et al.* 2021).

*Sexual morph:* *Ascomatal bases* globose, light to golden brown; necks light brown, cylindrical, tapering towards apex, flexible. *Ostiolar hyphae* present, slightly divergent, hyaline. *Ascospores* hyaline, 1-celled, no sheath, short cylindrical to bean-shaped.

*Asexual morph:* Sporothrix-like; *conidiophores* micronematous, mononematous, hyaline; *conidiogenous cells* hyaline, denticulate; *conidia* hyaline, 1-celled, oblong, occasionally producing secondary spores hyaline, 1-celled, obovoid.

*Type species:* *Chrysosphaeria jan-nelii* W.J. Nel *et al.*, Mycologia 113: 1206. 2021. MycoBank MB 837566.

*Notes:* Unlike most species in the *Ophiostomatales*, which occur on wood and have associations with bark or ambrosia beetles, *Chrysosphaeria* was isolated from abandoned combs of the fungus-growing termite *Macrotermes natalensis*.

## **Dryadomyces (Lineage V)**

***Dryadomyces*** Gebhardt, Mycol. Res. 109: 693. 2005. MycoBank MB 28937, *emend.* Z.W. de Beer & M. Procter Fig 7A, B.

*Etymology:* 'dryads, the tree nymphs in Greek mythology; referring to the habitat of these fungi in woody plants' (Gebhardt *et al.* 2005).

*Sexual morph:* Unknown.

*Asexual morph:* Colony confluent, mucilaginous. *Conidiophores* single or aggregated in sporodochia, macronematous, mononematous, hyaline, smooth. *Conidiogenous cells* monilliod or oblong, sympodial, with denticles or inconspicuous scars. *Conidia* hyaline to subhyaline,

1-celled, globose to subglobose, obovoid to pyriform with truncate base, smooth, producing secondary spores. *Aleuriospores* absent or present, hyaline, globose to subglobose, terminal.

*Type species:* *Dryadomyces amasae* Gebhardt, Mycol. Res. 109: 693. 2005. MycoBank MB 369332.

*Notes:* Based on our analyses, *Dryadomyces* now includes five ambrosia beetle-associated species, previously described in either *Ambrosiella*, *Raffaelea* or *Dryadomyces* (Gebhardt *et al.* 2005, De Beer & Wingfield 2013). *Raffaelea sulphurea* was isolated from hardwood-infesting ambrosia beetles, as was its sister species, *R. montetyi* (Massoumi Alamouti *et al.* 2009). Two Asian species in this complex, *R. quercivora* from Japan and *R. quercus-mongolicae* from Korea, have been implicated in contributing to the death of large numbers of *Quercus* spp. in their native ranges (Dreaden *et al.* 2014).

The fifth species in Clade V of our analyses (Fig. 5), *Dryadomyces amasae*, was initially described as the type species of the monotypic genus *Dryadomyces*. It was isolated from the ambrosia beetle *Amasae concitatus* in Taiwan (Gebhardt *et al.* 2005). Although the conidia of *D. amasae* differ from other *Raffaelea* species, Harrington *et al.* (2008) suggested that all ambrosial fungi in the *Ophiostomatales* should be treated in *Raffaelea*, until further studies revealed the taxonomic identities of these fungi. The more robust phylogenies constructed by Massoumi Alamouti *et al.* (2009) revealed a monophyletic lineage including *D. amasae*, *R. sulphurea* and *R. montetyi*. However, Harrington *et al.* (2010) treated *D. amasae* in *Raffaelea*, not considering the differences between conidia of *D. amasae* and other *Raffaelea* species as sufficient to separate *Dryadomyces* from *Raffaelea*.

De Beer & Wingfield (2013) named the lineage containing *R. amasae*, *R. montetyi*, *R. sulphurea*, *R. quercus-mongolicae* and *R. quercivora* as the *R. sulphurea* complex, referring to the oldest of the five described species. This complex grouped within *Leptographium s.l.* in their phylogenies. They did, however, note that the *R. sulphurea* complex is most probably not part of the larger *Leptographium s.l.*, but their data were insufficient to show otherwise. They suggested that when more robust phylogenies support the *R. sulphurea* complex as a monophyletic lineage separate from other genera, *Dryadomyces* would be a suitable name as the complex includes *D. amasae*.

Dreaden *et al.* (2014) investigated the monophyly of *Raffaelea* and showed that the *R. sulphurea* complex grouped close to isolates of *E. vermicola* within *Leptographium s.l.* as defined by De Beer & Wingfield (2013). They concluded that a larger study including additional *Leptographium* and *Raffaelea* species should provide clarity on the placement of these outlying *Raffaelea* lineages.

The *R. sulphurea* complex consistently formed a well-defined lineage distinct from *Leptographium* in our phylogenies. This supported re-instating the name *Dryadomyces* for this lineage. The description of *Dryadomyces* by Gebhardt *et al.* (2005) is emended here to accommodate other species in this lineage.

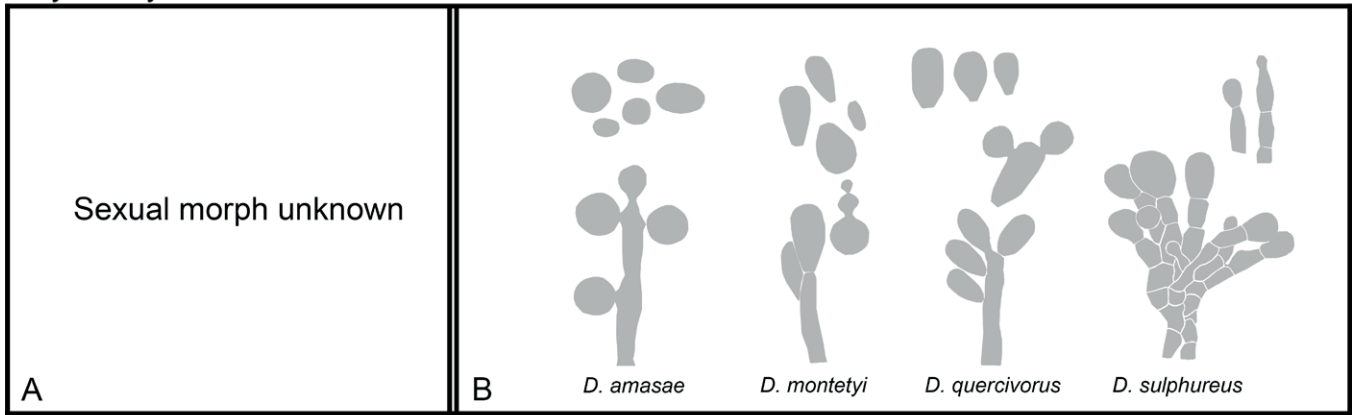
### **New combinations:**

**1) *Dryadomyces montetyi*** (M. Morelet) M. Procter & Z.W. de Beer, *comb. nov.* MycoBank MB 840313.

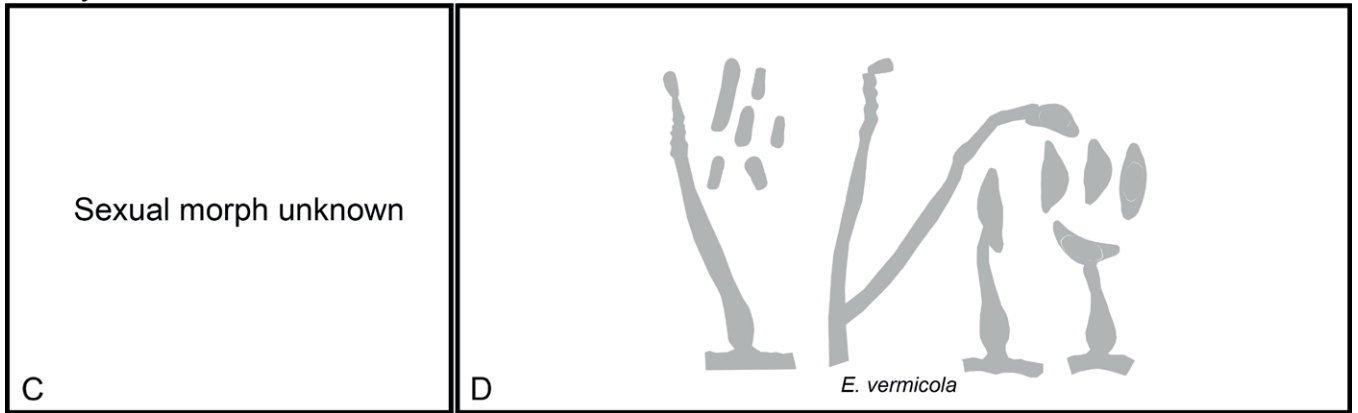
*Basionym:* *Raffaelea montetyi* M. Morelet, Ann. Soc. Sci. Nat. Archéol. Toulon Var 50: 189. 1998. MycoBank MB 445315.

*Description:* Morelet (1998: 189–191, fig. A).

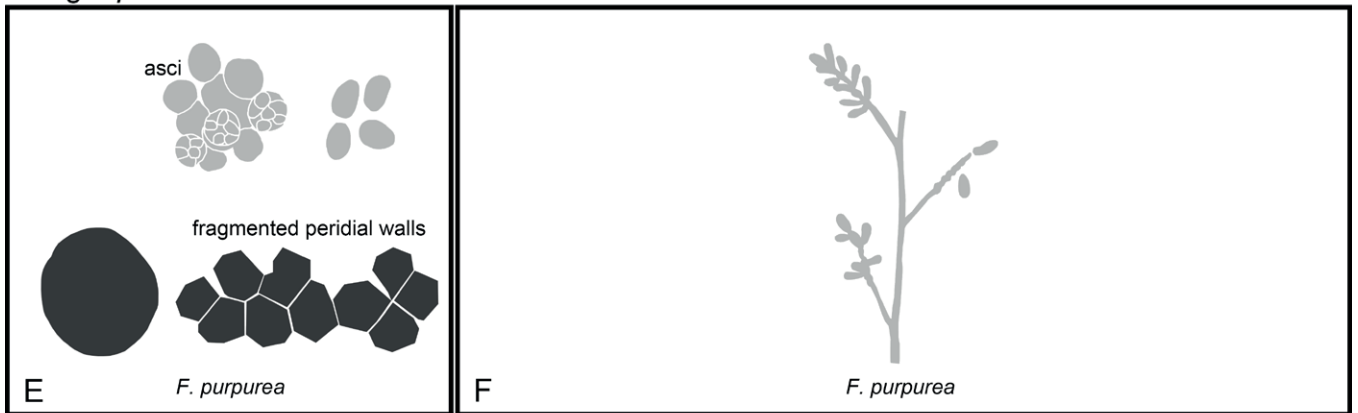
*Dryadomyces*



*Esteya*



*Fragosphaeria*



*Graphilbum*

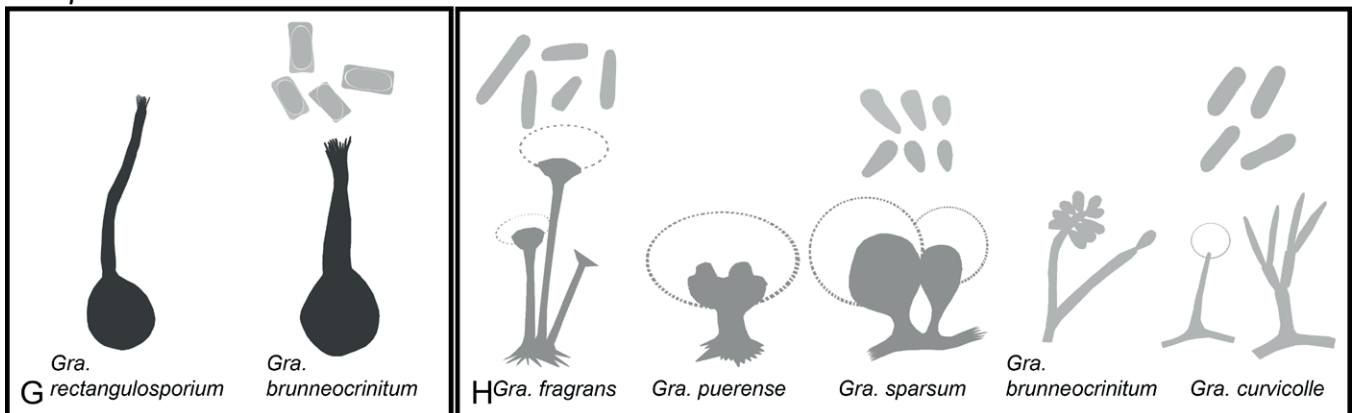


Fig. 7. Genera of the *Ophiostomatales* redrawn from published images with sexual morphs (if known) on the left and asexual morphs on the right. A, B. *Dryadomyces*. C, D. *Esteya*. E, F. *Fragosphaeria*. G, H. *Graphilbum*. (Pale grey shading reflects hyaline to subhyaline colouration, medium-tone grey brown to dark brown and dark grey reflects fuscous black to dark black colouration).

*Phylogenetic data:* Gebhardt *et al.* (2005), Massoumi Alamouti *et al.* (2009), Harrington *et al.* (2010), Matsuda *et al.* (2010), De Beer & Wingfield (2013), Dreaden *et al.* (2014), Musvuugwa *et al.* (2015), De Beer *et al.* (2016a, b), Vanderpool *et al.* (2017), Li *et al.* (2018), Saucedo-Carabez *et al.* (2018).

*Notes:* It forms part of *Dryadomyces* (Fig. 5), previously designated as the *R. sulphurea* complex (De Beer & Wingfield 2013).

**2) *Dryadomyces quercivorus*** (Kubono & Shin. Ito) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840316.

*Basionym:* *Raffaelea quercivora* Kubono & Shin. Ito, Mycoscience 43: 256. 2002. MycoBank MB 483997.

*Description:* Kubono & Ito (2002: 256–259, figs 1–11).

*Phylogenetic data:* Kim *et al.* (2009), Seo *et al.* (2010), Matsuda *et al.* (2010), Endoh *et al.* (2011), Dreaden *et al.* (2014), Musvuugwa *et al.* (2015), Simmons *et al.* (2016), Van der Linde *et al.* (2016), De Beer *et al.* (2016a, b), Vanderpool *et al.* (2017), De Errasti *et al.* (2018), Li *et al.* (2018), Saucedo-Carabez *et al.* (2018).

*Notes:* *Dryadomyces quercivorus* groups in *Dryadomyces* and was previously accommodated in the *R. sulphurea* complex (Fig. 5; De Beer & Wingfield 2013, De Errasti *et al.* 2018, Li *et al.* 2018, Saucedo-Carabez *et al.* 2018).

**3) *Dryadomyces quercus-mongolicae*** (K.H. Kim *et al.*) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840318.

*Basionym:* *Raffaelea quercus-mongolicae* K.H. Kim *et al.*, Mycotaxon 110: 193. 2009. MycoBank MB 515072.

*Description:* Kim *et al.* (2009: 193–195, fig. 2).

*Phylogenetic data:* Kim *et al.* (2009), Seo *et al.* (2010), De Beer *et al.* (2016a), Vanderpool *et al.* (2017), De Errasti *et al.* (2018), Li *et al.* (2018), Saucedo-Carabez *et al.* (2018).

*Notes:* *Dryadomyces quercus-mongolicae* groups in *Dryadomyces*, and was formerly in the *R. sulphurea* complex (Fig. 5; De Beer & Wingfield 2013, Li *et al.* 2018, Saucedo-Carabez *et al.* 2018).

**4) *Dryadomyces sulphureus*** (L.R. Batra) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840321.

*Basionym:* *Ambrosiella sulphurea* L.R. Batra, Mycologia 59: 992. 1967. MycoBank MB 326145.

*Synonyms:* *Raffaelea sulphurea* (L.R. Batra) T.C. Harr., Mycotaxon 111: 353. 2010. MycoBank MB 515298.

*Cephalosporium luteum* Verrall, J. Agric. Res. 66: 141. 1943. MycoBank MB 284848.

*Description:* Batra (1967: 992–998, figs 20, 21, 26–29), Verrall (1943: 141, 142, fig 4).

*Phylogenetic data:* Cassar & Blackwell (1996), Rollins *et al.* (2001), Gebhardt *et al.* (2005), Massoumi Alamouti *et al.* (2009), Harrington *et al.* (2010), Matsuda *et al.* (2010), De Beer & Wingfield (2013), Dreaden *et al.* (2014), Musvuugwa *et al.* (2015), Simmons *et al.* (2016), De Beer *et al.* (2016a, b), Vanderpool *et al.* (2017), Saucedo-Carabez *et al.* (2018).

*Notes:* This taxon groups in *Dryadomyces* (Fig. 5), previously designated as the *R. sulphurea* species complex (De Beer & Wingfield 2013), and has a heterotypic synonym, *Cephalosporium luteum* (Verrall 1943). Gharabigloozare (2015) proposed *C. luteum* as conspecific with *R. sulphurea*. These two species were isolated from *Xyleborinus saxeseni* (syn. *Xyleborus pecanici*) and their galleries. The culture morphologies and conidial dimensions of Batra (1967) and Verrall (1943) match and we support their conspecificity. In terms of nomenclatural priority, *Cephalosporium luteum* (1943) has precedence over *A. sulphurea* (1967) and the former epithet has a priority over the latter as a basionym. However, since De Beer & Wingfield (2013) introduced *R. sulphurea* complex, the name *R. sulphurea* has been widely used and recognised, and we have chosen not to introduce a new epithet for this species.

## **Esteya (Lineage IV)**

***Esteya*** J.Y. Liou *et al.*, Mycol. Res. 103: 243. 1999. MycoBank MB 28256, **emend.** Z.W. de Beer & M. Procter Fig. 7C, D.

*Etymology:* 'Named in honour of Prof. Ralph H. Estey (Macdonald College, McGill University, Canada), in recognition of his contribution to the study of nematophagous fungi and nematology' (Liou *et al.* 1999).

*Sexual morph:* Unknown.

*Asexual morph:* *Conidiophores* macronematous, mononematous, simple, subhyaline to pigmented, smooth to verrucous. *Conidiogenous cells* flask-shaped. *Conidia* hyaline, 1-celled, smooth, asymmetrically ellipsoidal in face view, concave, lunate in side view, ends moderately apiculate, with a layer of adhesive mucus on concave surface, containing ovoid endospore-like structures. Hyalorhinoclastiella-like; *conidiophores* macronematous, mononematous, simple or branched, subhyaline to pigmented, smooth to verrucous; *conidiogenous cells* cylindrical to subulate; *conidia* hyaline, 1-celled, cylindrical, smooth.

*Type species:* *Esteya vermicola* J.Y. Liou *et al.*, Mycol. Res. 103: 243. 1999. MycoBank MB 450702.

*No other species known.*

*Notes:* The genus *Esteya* was first described by Liou *et al.* (1999) and includes the single species, *E. vermicola* (Wang *et al.* 2015). *Esteya vermicola* produces two different types of conidia depending on abiotic and biotic factors, with one of the forms lethal to nematodes when consumed (Liou *et al.* 1999). This species was first isolated from the pine wood nematode *Bursaphelenchus xylophilus*. It is the only nematode-associated fungus in the *Ophiostomatales*, clearly distinguishing *Esteya* from other genera in the Order. Wang *et al.* (2008) discovered another isolate of *E. vermicola*, and upon performing a BLAST search in GenBank found that members of the *Ophiostomatales* were the closest phylogenetic relatives. They subsequently performed molecular phylogenetic analyses including various *Ophiostomatales* species and found that *Esteya* grouped close to but separately from a clade containing two *Leptographium* and two *Grosmannia* species, and distinct from any other genus in the *Ophiostomatales*. The phylogenies of De Beer & Wingfield (2013) did not resolve the generic placement of *Esteya* in the *Ophiostomatales*, showing that *Esteya* grouped within *Leptographium* s.l. based on both ITS and

LSU sequence data. These authors chose not to reduce *Esteya* to synonymy with *Leptographium* and recommended that *Esteya* should not be treated in *Leptographium* but be retained as a distinct genus until further studies could be conducted on the group. Later studies using LSU data again placed *Esteya* in *Leptographium* s.l. (Musvuugwa et al. 2015, De Beer et al. 2016a). Dreaden et al. (2014) used SSU, LSU and  $\beta$ -*tub* genes, which also placed *Esteya* in *Leptographium* s.l. In the phylogenies of the *TEF-1 $\alpha$*  and  $\beta$ -*tub* genes generated by Wang et al. (2014), the separate treatment of *Esteya* from *Leptographium* s.l. was well supported.

In our datasets, *Esteya* grouped within what was previously known as *Leptographium* s.l. The separation of *Grosmannia* and *Leptographium* based on our data, allows the recognition of *Esteya* as a distinct genus, forming a well-supported clade including two of the known *E. vermicola* isolates. Our data did not include the type specimen of *E. vermicola*, because cultures of this fungus were not available in the culture collections from which isolates were sought. It is interesting that a nematode-associated fungus groups within a family of fungi not associated with nematodes. The discovery of other *Esteya* isolates may shed light on the evolution of this unique lifestyle within the *Ophiostomatales*.

### **Fragosphaeria (Lineage XXI)**

**Fragosphaeria** Shear, Mycologia 15: 124. 1923. MycoBank MB 2011, **emend.** Z.W. de Beer & M. Procter Fig. 7E, F.

**Etymology:** Name is derived from the word “fragor” meaning “breaking to pieces” and “sphaera” (Shear 1923), referring to the spherical ascomata of the two species in the genus that easily break into fragments when handled.

**Sexual morph:** *Ascomatal* bases dark, globose, cleistothecial, walls easily fragmented. *Asci* subglobose. *Ascospores* yellowish-brown, 1-celled, broadly bean-shaped.

**Asexual morph:** *Conidia* hyaline, 1-celled, oblong to ellipsoidal, subalantoid, inequilateral.

**Type species:** *Fragosphaeria purpurea* Shear, Mycologia 15: 124. 1923. MycoBank MB 275760.

**Other species:** Listed in Table 1.

**Notes:** *Fragosphaeria* was first associated with the *Ophiostomatales* when a study by Suh & Blackwell (1999) showed that *F. purpurea*, the type species of this genus, grouped with some *Ophiostoma* species. The genus currently includes only two species, *F. purpurea* (Shear 1923) and *F. reniformis* (Saccardo 1881). The latter species was originally described in *Cephalotheca*, which Chesters (1935) reduced to synonymy with *Fragosphaeria* based on the similarities between *F. purpurea*, *Cephalotheca sulfurea* and *C. reniformis*. Malloch & Cain (1970) reinstated *Fragosphaeria*, transferring *Cephalotheca reniformis* to *Fragosphaeria*.

Both *Fragosphaeria* species are associated with stained wood within and surrounding bark beetle galleries in hardwoods and have been isolated in Britain and North America (Chesters 1935, De Beer & Wingfield 2013). Drawings by Chesters (1935) show a sporothrix-like asexual morph and allantoid ascospores produced by the cephalothecoid ascomata, which link this genus with other ophiostomatalean genera. However, the spherical cephalothecoid ascomata distinguish it from other *Ophiostomatales* (De Beer &

Wingfield 2013). A study by Yaguchi et al. (2006) showed that there was no evident relationship between species of *Cephalotheca* and *Fragosphaeria* and confirmed that the two *Fragosphaeria* isolates group together. Our data confirm the treatment of *Fragosphaeria* as a distinct, monophyletic genus in the *Ophiostomatales*.

### **Graphilbum (Lineage VIII)**

**Graphilbum** H.P. Upadhyay & W.B. Kendr., Mycologia 67: 800. 1975. MycoBank MB 8393, **emend.** Z.W. de Beer et al. In *The Ophiostomatoid Fungi: Expanding Frontiers*: 268. 2013. Fig. 7G, H.

**Etymology:** *Graphilbum* was described as the hyaline analogue of the genus *Graphium* (Upadhyay & Kendrick 1975). *Graphium* was later shown to form part of the *Microascales* (Okada et al. 1998), while *Graphilbum* resides in the *Ophiostomatales* (Zipfel et al. 2006). Although somewhat of a misnomer, the name *Graphilbum* remains valid and represents a distinct genus in the *Ophiostomatales*.

**Sexual morph:** *Ascomatal* bases globose, subglobose, black; necks dark brown to black, nearly cylindrical, straight or slightly curved. *Ostiolar hyphae* present or absent, parallel or divergent. *Asci* evanescent, broadly clavate to subglobose. *Ascospores* hyaline, 1-celled, cylindrical to oblong in side view, globose in end view, enclosed in rectangular sheath.

**Asexual morph:** *Conidiophores* micronematous, semimacronematous, macronematous, mononematous, synnematous, branched, unbranched. Hyalorhinocladia-like; *conidiophores* simple or sparingly branched; *conidiogenous cells* sympodial, subulate; *conidia* hyaline, 1-celled, cylindrical or clavate to broadly clavate, oblong or ellipsoidal, sometimes slightly curved. Pesotum-like; stipes pale to dark pigmented, biverticillate; *conidiogenous cells* sympodial.

**Type species:** *Graphilbum sparsum* H.P. Upadhyay & W.B. Kendr., Mycologia 67: 800. 1975. MycoBank MB 314730.

**Other species:** Listed in Table 1.

**Notes:** *Graphilbum* was originally described to accommodate the asexual morph of some *Ophiostoma* (then *Ceratocystis*) species (Upadhyay & Kendrick 1975). Okada et al. (1998) treated *Graphilbum* together with other genera in the *Ophiostomatales*, which have synnematous asexual morphs, as a synonym of *Pesotum*. However, De Beer et al. (2013a) showed that the type species of *Pesotum*, *O. ulmi*, grouped within *Ophiostoma* s.s., while the type species of *Graphilbum*, *O. sparsum*, formed a lineage distinct from *Ophiostoma* s.s. They consequently reduced *Pesotum* to synonymy with *Ophiostoma*, and reinstated *Graphilbum* with *Gra. sparsum* as the type species, including seven additional species in the genus. *Graphilbum* species are characterised by Type E ascospores (Fig. 3H) and either a hyalorhinocladia- or pesotum-like asexual morph (Fig. 3A, C; *sensu* De Beer & Wingfield 2013). This is with the exception of *Gra. tsugae* that produces a continuum of hyalorhinocladia-like and pesotum-like asexual morphs. *Graphilbum* species are commonly found in galleries of conifer-infesting bark beetles in the Northern Hemisphere (De Beer et al. 2013b, Romón et al. 2014a, Reid & Hausner 2015, Jankowiak et al. 2020).

In our analyses, *Graphilbum* formed a well-supported monophyletic lineage, distinct from other genera. Interestingly,



*Ophiostoma pusillum* consistently grouped with *Graphilbum*, supporting previous suggestions that the species might form part of this genus (De Beer & Wingfield 2013).

**New combination:**

**1) *Graphilbum pusillum*** (Masuya) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840324.

*Basionym:* *Ophiostoma pusillum* Masuya, *Mycoscience* 44: 302. 2003. MycoBank MB 489291.

*Description:* Masuya *et al.* (2003: 302, figs 1–10).

*Phylogenetic data:* Fig. 5.

*Notes:* Masuya *et al.* (2013) treated this species as part of the *O. ips* complex based on morphology. However, due to morphological similarities with the fungus known as *Ophiostoma nigrum* and *Ceratocystis tubicollis* (Masuya *et al.* 2003), De Beer *et al.* (2013b) suggested that it may rather belong in *Graphilbum*. Both *O. nigrum* (now *Gra. nigrum*) and *C. tubicollis* (now *Gra. tubicolle*) were treated in *Graphilbum* by De Beer *et al.* (2013b), and our sequence data also confirm the placement of *O. pusillum* in this genus (Fig. 5). The name should not be confused with *S. pusilla* U. Braun & Crous [= *Quambalaria pusilla* (U. Braun & Crous) J.A. Simpson] (De Beer *et al.* 2006) or *Graphium pusillum* (Wallr.) Sacc. (De Beer *et al.* 2013b).

***Grosmannia* (Lineage II)**

***Grosmannia*** Goid., *Boll. Staz. Patol. Veg. Roma* 16: 27. 1936. MycoBank MB 2141, **emend.** Z.W. de Beer & M. Procter. Fig. 8A–D.

*Etymology:* Goidànich (1935) named the genus after the German forest pathologist, Helene Grosmann, later Francke-Grosmann (1900–1990), who described both the asexual morph (as *Leptographium penicillatum* Grosmann) and the sexual morph (as *Ceratostomella penicillata* Grosmann) of the type species of this genus.

*Synonym:* *Verticicladiella* S. Hughes, *Canad. J. Bot.* 31: 653. 1953. MycoBank MB 10394. [Type species *V. abietina* (Peck) S. Hughes].

*Sexual morph:* *Ascomatal bases* subglobose to globose, black; *necks* nearly cylindrical, straight or slightly curved, black. *Ostiole hyphae* absent or present, divergent or variable. *Asci* evanescent. *Ascospores* hyaline, 1-celled, enclosed in sheath or not, endospores orange segment-shaped in side view, cylindrical in face view, globose to ellipsoidal in end view.

*Asexual morph:* *Conidiophores* macronematous, micronematous, mononematous, synnematous, singly or in groups. *Hyalorhinocladiella*-like; *conidia* hyaline, 1-celled, oblong to obovoid. *Leptographium*-like; *conidiophores* branched; *stipes* pale brown, branches pale brown, becoming hyaline towards apex, bases simple or rhizoid-like; *conidiogenous cells* hyaline; *conidia* hyaline, 1-celled, oblong, broadly ellipsoidal to slightly obovoid, sometimes allantoid, narrowly obovoid to clavate, straight or distinctly curved. *Pesotum*-like; *conidiophores* single or in groups; *conidia* hyaline, oblong, 1-celled. *Sporothrix*-like; *conidiophores* simple; *conidiogenous cells* hyaline, cylindrical, sympodial, denticulate; *conidia* hyaline, 1-celled, oblong, ovoid to ellipsoidal, clavate, sometimes developing into larger ramoconidia,

producing secondary spores. *Ramoconidia* hyaline, 1-celled, clavate. Single ascospore cultures yeasty, budding hyaline conidia, ovoid to elongate, colony later darkened. *Aleuriospores* hyaline or pigmented, globose to subglobose, oval to ellipsoid.

*Type species:* *Grosmannia penicillata* (Grosmann) Goid., *Boll. Staz. Patol. Veg. Roma* 16: 46. 1936. MycoBank MB 253870.]

*Notes:* *Grosmannia* was originally erected by Goidànich (1935) to accommodate sexual species of *Ceratostomella* with leptographium-like asexual morphs (Davidson 1942). The genus was later treated as synonym of both *Ophiostoma* (Siemaszko 1939) and *Ceratocystis* (Bakshi 1951). Zipfel *et al.* (2006) showed that *Ophiostoma* and *Grosmannia* were distinct from each other based on ITS and LSU sequences, and separated the two genera based on these and morphological differences. However, the focus of the Zipfel *et al.* (2006) study was primarily on sexually reproducing species.

De Beer & Wingfield (2013) included sequence data for many more asexual *Leptographium* spp. in their study and showed that *Leptographium* and *Grosmannia* spp. grouped together, along with other previously unassociated *Ophiostoma* spp. They applied the older name, *Leptographium* to this group, rather than *Grosmannia*, which following the dual nomenclature system (McNeill *et al.* 2012) had preference because it was considered a sexual genus (De Beer & Wingfield 2013). They referred to the lineage as *Leptographium s.l.*, even though the lineage did not show strong monophyletic support. The type species of *Grosmannia* (*G. penicillata*) grouped in a lineage distinct from the type species of *Leptographium* (*L. lundbergii*). However, they recommended that novel species grouping in what they referred to as the *G. penicillata* complex should be treated as *Grosmannia* species. This was until more robust analyses could confirm whether the *G. penicillata* complex should be treated as a distinct genus.

Based on the data emerging from the present study, we have reinstated *Grosmannia* as a genus distinct from *Leptographium*, for species that produce leptographium-like asexual morphs and have allantoid, hyaline and aseptate ascospores. These species are commonly associated with conifer-infesting bark beetles in the Northern Hemisphere (Jacobs & Wingfield 2001, Linnakoski *et al.* 2012). Based on our phylogenetic analyses, *Grosmannia* includes the fungus previously known as *G. penicillata* s.s. (referred to here as the *G. penicillata* complex), *G. abieticola* and *L. taigense* (Lineage C), and the newly recognised *G. grandifoliae* complex (Jankowiak *et al.* 2017).

***Species complexes:***

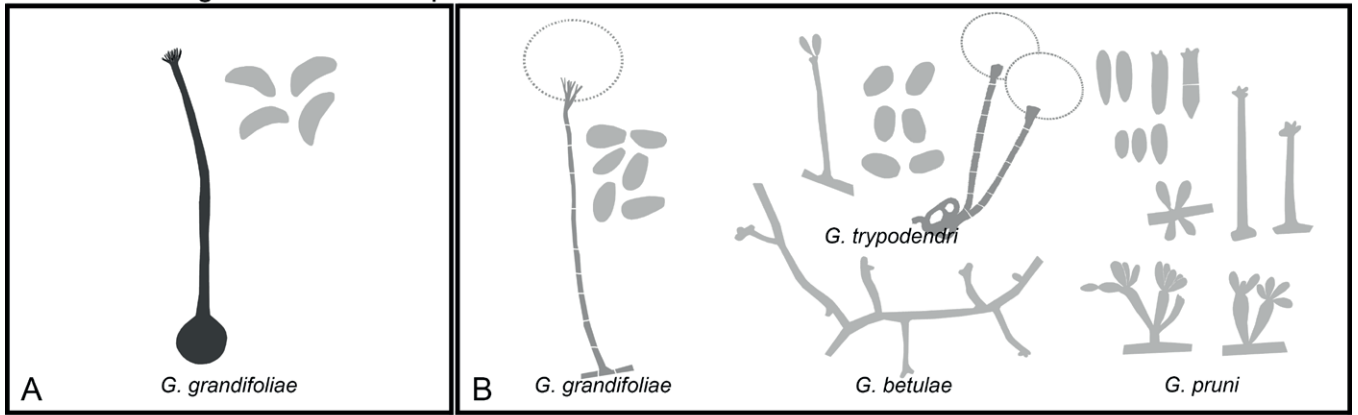
**The *G. penicillata* complex**

The *G. penicillata* complex as defined by Six *et al.* (2011), Linnakoski *et al.* (2012) and De Beer & Wingfield (2013) included 18 species. Our results and those emerging from other studies add another seven species to the complex within a well-supported lineage. All 25 species are associated in some way with conifer-infesting bark and ambrosia beetles in the Northern Hemisphere. The complex is named based on the first species in the complex to be described, *G. penicillata* [as *Ceratostomella penicillata* (Grosmann 1932)], which is also the type species of *Grosmannia*.

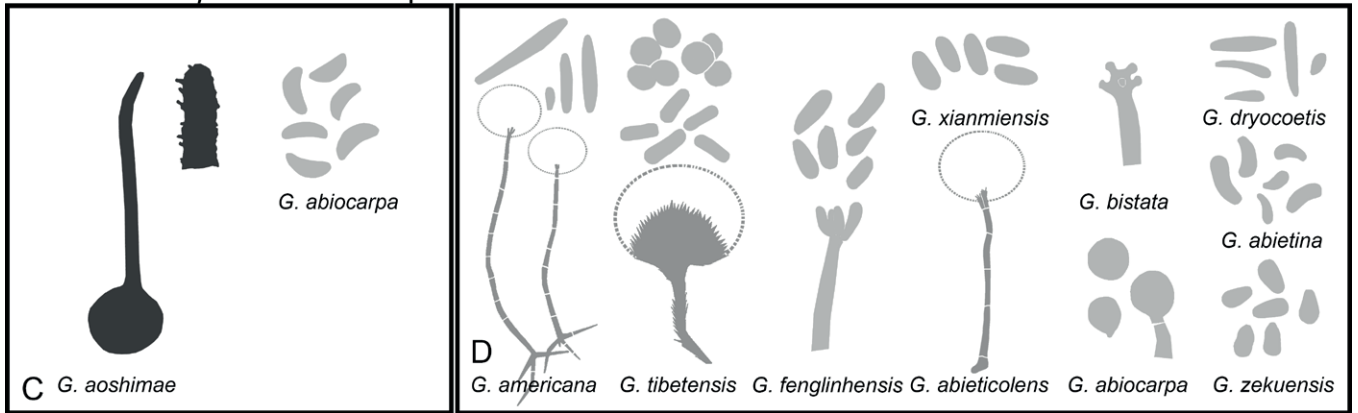
**The *G. grandifoliae* complex**

The second species complex included in our definition of *Grosmannia*, the *G. grandifoliae* complex, emerged when two new

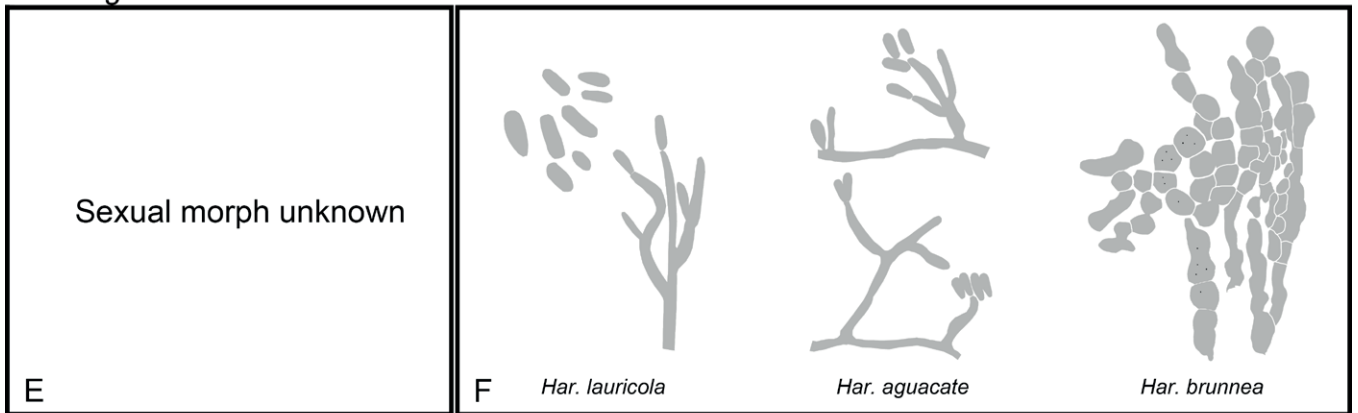
*Grosmannia grandifoliae* complex



*Grosmannia penicillata* complex



*Harringtonia*



*Hawksworthiomyces*

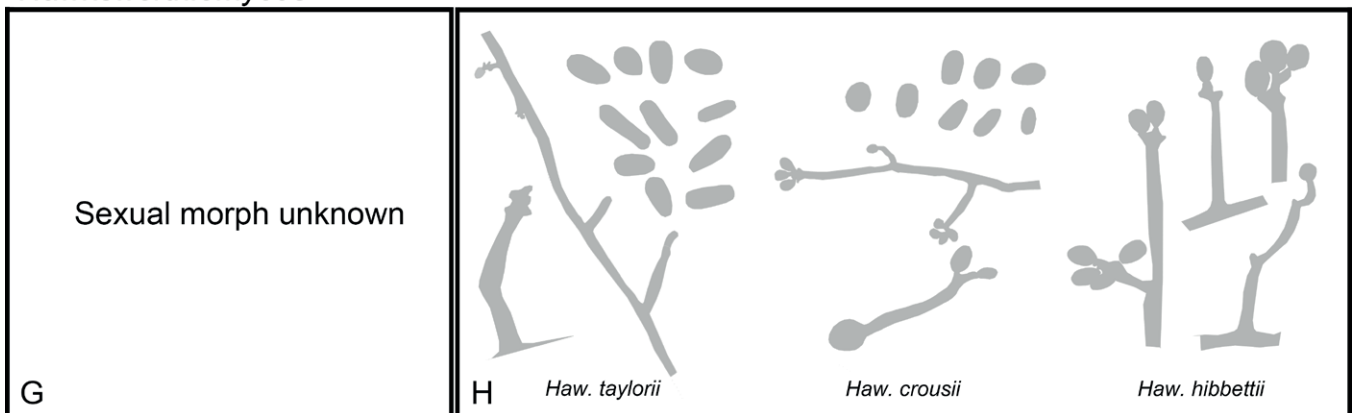


Fig. 8. Genera of the *Ophiostomatales* redrawn from published images with sexual morphs (if known) on the left and asexual morphs on the right. A, B. *Grosmannia grandifoliae* complex. C, D. *Grosmannia penicillata* complex. E, F. *Harringtonia*. G, H. *Hawksworthiomyces*. (Pale grey shading reflects hyaline to subhyaline colouration, medium-tone grey brown to dark brown and dark grey reflects fuscous black to dark black colouration).

species of *Leptographium* were described from Poland (Jankowiak *et al.* 2017). Both species formed a well-supported lineage with *G. grandifoliae* and *L. pruni*, sister to the *G. penicillata* complex. Prior to the description of the new species, *L. pruni* and *G. grandifoliae* did not form part of the *G. penicillata* complex or any of the other species complexes recognised by De Beer *et al.* (2013b) in *Leptographium s.l.* Jankowiak *et al.* (2017) suggested that *G. grandifoliae* should be the name-bearing species of this small complex, because it is the oldest known name among the species that it accommodates.

*Grosmannia grandifoliae* is the only species for which a sexual morph has been observed and that is characterised by ascomata with very long necks (Jacobs & Wingfield 2001). With the addition of the two new species from Poland, *L. trypodendri* and *L. betulae*, it became evident that this complex represents a well-supported hardwood-infesting lineage in *Grosmannia* (Fig. 5) (Jankowiak *et al.* 2017). *Leptographium trypodendri* was isolated mostly from *Trypodendron* (beetle) species and *L. betulae* in association with *Scolytus* species (Jankowiak *et al.* 2017). This is the first species complex in *Leptographium* and *Grosmannia* that accommodates only hardwood-infesting species (Jankowiak *et al.* 2017).

In our datasets, the *G. grandifoliae* complex grouped within Lineage II in all except the *TEF-1 $\alpha$*  tree (Fig. S3) where it grouped with Group C (below) among species complexes in *Leptographium*. The clear ecological distinction and the well-supported monophyletic lineage of the *G. grandifoliae* complex, supports its treatment as novel genus. In the future, this will need to be verified using more robust phylogenies including additional gene regions, and if possible, inclusion of a greater number of species in the complex.

### Group C

In the phylogenies of Linnakoski *et al.* (2012), *L. taigense* grouped in a distinct lineage between the *G. grandifoliae* and *G. penicillata* complexes. In the LSU tree generated by De Beer & Wingfield (2013), *L. taigense* also grouped outside of the *G. penicillata* complex, close to, but not in a well-supported lineage with *G. abieticola*. With the additional gene regions included in this study, *L. taigense* and *G. abieticola* emerged together in a well-supported lineage distinct from, but between the two complexes defined above. Both these species are associated with conifers, as is true for all species in the *G. penicillata* complex. For the present, we have chosen to treat them in *Grosmannia*, but inclusion of newly discovered species in this lineage in the future could justify the description of a new genus to accommodate these species.

#### New combinations:

**1) *Grosmannia abieticolens*** (K. Jacobs & M.J. Wingf.) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840331.

*Basionym:* *Leptographium abieticolens* K. Jacobs & M.J. Wingf., *Mycoscience* 41: 599. 2000. MycoBank MB 466545.

*Description:* Jacobs & Wingfield (2001: 46–48, figs 19–21).

*Phylogenetic data:* Jacobs *et al.* (2001b), Kim *et al.* (2004, 2005a), Masuya *et al.* (2004), Massoumi Alamouti *et al.* (2006), Paciura *et al.* (2010), Six *et al.* (2011), Duong *et al.* (2012), De Beer & Wingfield (2013), Huang & Chen (2014), Musvuugwa *et al.* (2015), Chang *et al.* (2019).

*Notes:* Sexual morph unknown. While it was not included in our study, *G. abieticolens* groups in the *G. penicillata* complex based

on previously published data (Six *et al.* 2011, De Beer & Wingfield 2013, Chang *et al.* 2019). The name should not be confused with *Grosmannia abieticola* that formed part of Group C in our analyses.

*Notes on Grosmannia abietina:* Sexual morph unknown. *Grosmannia abietina* groups in the *G. penicillata* species complex (Fig. 4; Six *et al.* 2011, Linnakoski *et al.* 2012, De Beer & Wingfield 2013). The species should not be confused with *Sporothrix abietina*, that resides in *Sporothrix*. Jacobs *et al.* (1998) proposed the synonymy of *G. engelmannii* (as *L. engelmannii*) with *G. abietina* (as *L. abietinum*), which was supported by Jacobs & Wingfield (2001). In our analyses, an isolate of *L. engelmannii* (CMW 759) grouped with *G. abietina* in the *TEF1- $\alpha$*  tree (Fig. S3) and separate from that species in the LSU tree (Fig. S1).

**2) *Grosmannia altior*** (Paciura, Z.W. de Beer & M.J. Wingf.) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840369.

*Basionym:* *Leptographium altius* Paciura *et al.*, *Persoonia* 25: 106. 2010. MycoBank MB 516740.

*Description:* Paciura *et al.* (2010: 106, fig. 7h–m).

*Phylogenetic data:* Paciura *et al.* (2010), Duong *et al.* (2012), Linnakoski *et al.* (2012), De Beer & Wingfield (2013), Liu *et al.* (2017), Chang *et al.* (2019).

*Notes:* Sexual morph unknown. This species forms part of the *G. penicillata* complex based on previously published data (Paciura *et al.* 2010, Linnakoski *et al.* 2012, De Beer & Wingfield 2013, Liu *et al.* 2017, Chang *et al.* 2019).

**3) *Grosmannia betulae*** (Jankowiak *et al.*) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840370.

*Basionym:* *Leptographium betulae* Jankowiak *et al.*, *Antonie van Leeuwenhoek* 110: 1550. 2017. MycoBank MB 821670.

*Description:* Jankowiak *et al.* (2017: 1550, fig. 6).

*Phylogenetic data:* Jankowiak *et al.* (2017, 2018).

*Notes:* Sexual morph unknown. Groups in the *G. grandifoliae* species complex (Fig. 5; Jankowiak *et al.* 2017).

**4) *Grosmannia curviconidia*** (Paciura *et al.*) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840373.

*Basionym:* *Leptographium curviconidium* Paciura *et al.*, *Persoonia* 25: 104. 2010. MycoBank MB 516739.

*Description:* Paciura *et al.* (2010: 104–105, figs 7a–g).

*Phylogenetic data:* Paciura *et al.* (2010), Duong *et al.* (2012), Linnakoski *et al.* (2012), De Beer & Wingfield (2013), Huang & Chen (2014), Musvuugwa *et al.* (2015), Jankowiak *et al.* (2017, 2018), Liu *et al.* (2017), Chang *et al.* (2019).

*Notes:* Sexual morph unknown. *Grosmannia curviconidia* groups in the *G. penicillata* species complex (Fig. 5; Linnakoski *et al.* 2012, De Beer & Wingfield 2013, Huang & Chen 2014, Musvuugwa *et al.* 2015, Jankowiak *et al.* 2017, 2018, Liu *et al.* 2017, Chang *et al.* 2019).

**5) *Grosmannia euphyes*** (K. Jacobs & M.J. Wingf.) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840376.

*Basionym:* *Leptographium euphyes* K. Jacobs & M.J. Wingf., Mycol. Res. 105: 497. 2001. MycoBank MB 467761.

*Descriptions:* Jacobs *et al.* (2001c: 496–498, figs 15–21), Jacobs & Wingfield (2001: 96–99, figs 70–72).

*Phylogenetic data:* Jacobs *et al.* (2001a), Kim *et al.* (2004, 2005a), Masuya *et al.* (2004), Massoumi Alamouti *et al.* (2006), Paciura *et al.* (2010), Six *et al.* (2011), Duong *et al.* (2012), De Beer & Wingfield (2013), Jankowiak *et al.* (2017, 2018), Liu *et al.* (2017), Chang *et al.* (2019).

*Notes:* Sexual morph unknown. This species grouped in the *G. penicillata* complex based on previous data (Six *et al.* 2011, De Beer & Wingfield 2013, Jankowiak *et al.* 2017, 2018, Liu *et al.* 2017, Chang *et al.* 2019).

**6) *Grosmannia fenglinhensis*** (R. Chang *et al.*) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840377.

*Basionym:* *Leptographium fenglinhense* R. Chang *et al.*, Persoonia 42: 67. 2018 (2019). MycoBank MB 825092.

*Description:* Chang *et al.* (2019: 66–67, fig. 21).

*Phylogenetic data:* Chang *et al.* (2019)

*Notes:* Sexual morph unknown. Groups in the *G. penicillata* species complex (Fig. 5; Chang *et al.* 2019).

**7) *Grosmannia gestamen*** (Errasti & Z.W. de Beer) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840381.

*Basionym:* *Leptographium gestamen* Errasti & Z.W. de Beer, Mycol. Prog. 15: 11. 2016. MycoBank MB 814177.

*Descriptions:* De Errasti *et al.* (2016: 11–13, fig. 7).

*Phylogenetic data:* De Errasti *et al.* (2016), Jankowiak *et al.* (2017, 2018), Chang *et al.* (2019).

*Notes:* Sexual morph unknown. This species grouped close to *G. taigensis* (as *L. taigense*) in the phylogenies of Jankowiak *et al.* (2017) and Chang *et al.* (2019), and with *G. abieticola* (Jankowiak *et al.* 2018). We have consequently included it in *Grosmannia*, as part of the complex defined by the genus in group C (Fig. 5).

**8) *Grosmannia innermongolica*** (X.W. Liu *et al.*) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840384.

*Basionym:* *Leptographium innermongolicum* X.W. Liu *et al.*, Mycol. Prog. 16: 8. 2017. MycoBank MB 811204.

*Description:* Liu *et al.* (2017: 8–10, fig. 6).

*Phylogenetic data:* Liu *et al.* (2017), Chang *et al.* (2019).

*Notes:* Sexual morph unknown. This species grouped with *L. taigense* (Group C in Fig. 5) in the phylogenies of Liu *et al.* (2017) and Chang *et al.* (2019). It is consequently included in *Grosmannia* (Fig. 5).

**9) *Grosmannia pistaciae*** (Paciura *et al.*) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840385.

*Basionym:* *Leptographium pistaciae* Paciura *et al.*, Persoonia 25: 104. 2010. MycoBank MB 516738.

*Description:* Paciura *et al.* (2010: 104, figs 6g–l).

*Phylogenetic data:* Paciura *et al.* (2010), Duong *et al.* (2012), Linnakoski *et al.* (2012), De Beer & Wingfield (2013), Jankowiak *et al.* (2017, 2018), Liu *et al.* (2017), Chang *et al.* (2019).

*Notes:* Sexual morph unknown. *Leptographium pistaciae* has previously been shown to reside in the *G. penicillata* complex (Paciura *et al.* 2010, Linnakoski *et al.* 2012, De Beer & Wingfield 2013, Jankowiak *et al.* 2017, 2018, Liu *et al.* 2017, Chang *et al.* 2019).

**10) *Grosmannia pruni*** (Masuya & M.J. Wingf.) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840386.

*Basionym:* *Leptographium pruni* Masuya & M.J. Wingf., Mycologia 96: 553. 2004. MycoBank MB 488574.

*Description:* Masuya *et al.* (2004: 553–555, figs 1–16).

*Phylogenetic data:* Masuya *et al.* (2004, 2013), Massoumi Alamouti *et al.* (2006), Matsuda *et al.* (2010), Duong *et al.* (2012), De Beer & Wingfield (2013), De Errasti *et al.* (2016), Jankowiak *et al.* 2017, 2018), Chang *et al.* (2019).

*Notes:* Sexual morph unknown. This species grouped with *G. grandifoliae* and two other species to form the *G. grandifoliae* species complex (Jankowiak *et al.* 2017).

**11) *Grosmannia taigensis*** (Linnak. *et al.*) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840387.

*Basionym:* *Leptographium taigense* Linnak. *et al.*, Antonie van Leeuwenhoek 102: 387. 2012. MycoBank MB 564881.

*Description:* Linnakoski *et al.* (2012: 387–388, fig. 7).

*Phylogenetic data:* Linnakoski *et al.* (2012), De Beer & Wingfield (2013), Jankowiak *et al.* (2017, 2018), Liu *et al.* (2017), Chang *et al.* (2019).

*Notes:* Sexual morph unknown. This species grouped with *G. abieticola*, separated from other species complexes in *Grosmannia* (Fig. 5), based on LSU (Fig. S1) and *TEF1- $\alpha$*  (Fig. S3) sequence data.

**12) *Grosmannia trypodendri*** (Jankowiak *et al.*) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840388.

*Basionym:* *Leptographium trypodendri* Jankowiak *et al.*, Antonie van Leeuwenhoek 110: 1546. 2017. MycoBank MB 821669.

*Description:* Jankowiak *et al.* (2017: 1546–1550, fig. 5).

*Phylogenetic data:* Jankowiak *et al.* (2017, 2018).

*Notes:* Sexual morph unknown. Groups in the *G. grandifoliae* species complex (Fig. 5).

*Other species:* Listed in Table 1.

## Harringtonia (Lineage XI)

**Harringtonia** Z.W. de Beer & Procter, **gen. nov.** MycoBank MB 840400. Fig. 8E, F.

**Etymology:** Named for the American mycologist Prof. Thomas C. Harrington, who described the type species of this genus as *Raffaelea lauricola* (Harrington *et al.* 2008), and who has contributed substantially to our understanding of the biology and taxonomy of the *Ophiostomatales* (Harrington 1981, 1988, Harrington & Cobb 1987, Harrington *et al.* 2001, 2008, 2010, 2011).

**Synonym:** *Raffaelea lauricola* complex *sensu* Z.W. de Beer & M.J. Wingf., In *The Ophiostomatoid Fungi: Expanding Frontiers*: 34. 2013.

**Sexual morph:** Unknown.

**Asexual morph:** Colonies initially yeast-like at centre becoming cottony in 2 wk (*Har. lauricola*), cream-coloured, having submerged mycelium at margins, aging to dark green on MEA (*Har. aguacate*). Colonies when repeatedly subcultured forming a filamentous mycelium, with surface becoming finely tomentose (*Har. brunnea*). *Conidiophores* single or aggregated in sporodochia, hyaline, macronematous, semimacronematous, mononematous, simple or branched. *Conidiogenous cells* with inconspicuous annellations at point of conidial dehiscence. *Conidia* hyaline, 1-celled, oblong to ellipsoidal, obovoid, truncated at base, occasionally borne sessile, in some species producing secondary budding cells. Associated with ambrosia beetles.

**Type species:** *Harringtonia lauricola* (T.C. Harr. *et al.*) Z.W. de Beer & M. Procter, **comb. nov.** MycoBank MB 840401.

**Basionym:** *Raffaelea lauricola* T.C. Harr. *et al.*, *Mycotaxon* 104: 401. 2008. MycoBank MB 511590.

**Description:** Fraedrich *et al.* (2008: 219–220, fig. 5).

**Phylogenetic data:** Fraedrich *et al.* (2008), Harrington *et al.* (2008, 2010, 2011), Kim *et al.* (2009), Massoumi Alamouti *et al.* (2009), Matsuda *et al.* (2010), De Beer & Wingfield (2013), Dreaden *et al.* (2014), Musvuugwa *et al.* (2015), Simmons *et al.* (2016), De Beer *et al.* (2016a, b), Bateman *et al.* (2017), Vanderpool *et al.* (2018), Wingfield *et al.* (2017), Li *et al.* (2018), Saucedo-Carabez *et al.* (2018).

**Notes:** *Harringtonia lauricola* consistently forms a clade together with *Har. brunnea* and *Har. aguacate*, that has previously been referred to as the *R. lauricola* complex (De Beer & Wingfield 2013). This complex has always formed a monophyletic lineage close to, but distinct from *Raffaelea s.s.* in previous studies (Massoumi Alamouti *et al.* 2009, De Beer & Wingfield 2013, Dreaden *et al.* 2014, Simmons *et al.* 2016). When De Beer & Wingfield (2013) first defined this species complex, they chose *R. lauricola* as the name bearing species, because it is the best-known species in this complex. This is despite the fact that it was not the first species in the complex to be described. They suggested that this lineage would likely emerge as a new genus when more robust phylogenetic analyses were performed, as is the case in the present study.

In the analyses of our datasets, the *R. lauricola* complex grouped close to *Raffaelea s.s.* and together they formed a monophyletic

clade, although this relationship was not supported. Phylogenomic analyses conducted in the current study and previous studies (Nel *et al.* 2021; Vanderpool *et al.* 2018) showed that the *R. lauricola* complex and *Raffaelea s.s.* did not form a monophyletic lineage. Based on these results, we have removed the *R. lauricola* complex from *Raffaelea* and have described the complex as a new genus. While fully cogniscent of the fact that describing a new genus to accommodate an important tree pathogen might result in some early discomfort, this change is based on robust taxonomic data, not only from the present study. Failing to make this change perpetuates a taxonomically confused situation. In our view this decision will also provide opportunities to better understand the biology and evolutionary characteristics of two phylogenetically distinct and important groups of fungi.

All species in the *R. lauricola* complex produce raffaelea-like asexual morphs (De Beer & Wingfield 2013). *Harringtonia lauricola* is the causal agent of laurel wilt, a vascular wilt disease affecting *Lauraceae* species in the south-eastern USA. It is believed to have been introduced into the USA from Asia in the mycangia of *Xyleborus glabratus*, an ambrosia beetle invasive to the USA (Harrington *et al.* 2008). The other species in this complex are *Har. brunnea*, associated with ambrosia beetles infesting hardwoods (De Beer & Wingfield 2013), and *Har. aguacate*, originally isolated from avocado (*Persea americana*) (Simmons *et al.* 2016) and later shown to be vectored by *X. bispinatus* (Saucedo-Carabez *et al.* 2018).

### Other new combinations:

**1) *Harringtonia aguacate*** (D.R. Simmons *et al.*) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840402.

**Basionym:** *Raffaelea aguacate* D.R. Simmons *et al.*, *IMA Fungus* 7: 269. 2016. MycoBank MB 817170.

**Description:** Simmons *et al.* (2016: 269, fig. 2).

**Phylogenetic data:** Simmons *et al.* (2016), Vanderpool *et al.* (2018), Li *et al.* (2018), Saucedo-Carabez *et al.* (2018).

**Notes:** This species forms part of *Harringtonia* (Fig. 5), previously the *R. lauricola* complex (De Beer & Wingfield 2013).

**2) *Harringtonia brunnea*** (L.R. Batra) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840403.

**Basionym:** *Ambrosiella brunnea* L.R. Batra, *Mycologia* 59: 980. 1968 (1967). MycoBank MB 326140.

**Synonyms:** *Monilia brunnea* Verrall, *J. Agric. Res.* 66: 142. 1943. MycoBank MB 440994. *nom. illegit.*, Art. 53. 1.

*Raffaelea brunnea* (L.R. Batra) T.C. Harr., *Mycotaxon* 111: 351. 2010. MycoBank MB 515296.

**Descriptions:** Verrall (1943: 142–143, fig. 5), Batra (1967: 1004–1007, figs 43, 45, 46).

**Phylogenetic data:** Cassar & Blackwell (1996), Rollins *et al.* (2001), Gebhardt *et al.* (2005), Massoumi Alamouti *et al.* (2009), Harrington *et al.* (2010), Matsuda *et al.* (2010), De Beer & Wingfield (2013), Dreaden *et al.* (2014), Musvuugwa *et al.* (2015), De Beer *et al.* (2016a, b), Vanderpool *et al.* (2018), Wingfield *et al.* (2017), Li *et al.* (2018), Saucedo-Carabez *et al.* (2018).

**Notes:** This species forms part of *Harringtonia* (Fig. 5), previously the *R. lauricola* species complex (De Beer & Wingfield 2013).

This species should not be confused with *Monilia brunnea*, a soil inhabiting species.

## Hawksworthiomyces (Lineage XXII)

**Hawksworthiomyces** Z.W. de Beer *et al.*, Fungal Biol. 120: 1329. 2016. MycoBank MB 815685. Fig. 8G, H.

*Etymology*: 'Named for Dr David Hawksworth, in recognition of the leading role that he has played in guiding the global mycological community through the controversial and often challenging transition from a dual nomenclature to a One Fungus-One Name-based system' (De Beer *et al.* 2016b).

*Sexual morph*: Unknown.

*Asexual morph*: *Conidiophores* hyaline, micronematous to macronematous, mononematous, simple or branched. *Conidiogenous cells* hyaline, polyblastic, denticulate. *Conidia* hyaline, 1-celled, broadly ellipsoidal to cylindrical, producing secondary cells.

*Type species*: *Hawksworthiomyces lignivorus* (De Mey. *et al.*) Z.W. de Beer *et al.*, Fungal Biol. 120: 1329. 2016. MycoBank MB 815686.

*Other species*: Listed in Table 1.

*Notes*: *Hawksworthiomyces* was erected to accommodate *Sporothrix lignivora* (now *Haw. lignivora*) and three other species not previously associated with the *Ophiostomatales*. De Beer & Wingfield (2013) listed *S. lignivora* as "*incertae sedis*", as this species formed a lineage on its own, separate from other species in *Ophiostoma* and *Sporothrix*, even though its morphology resembled species of *Sporothrix* (De Meyer *et al.* 2008). BLAST searches on GenBank later revealed sequences from environmental studies and isolates from diversity studies with strong similarity to *S. lignivora*. Consequently, De Beer *et al.* (2016) proceeded to erect the new genus, *Hawksworthiomyces*, to incorporate *S. lignivora* and these "new" species. In the analyses of our data, *Haw. lignivora*, *Haw. taylorii*, *Haw. hibbettii* and *Haw. crousii* formed a well-supported monophyletic lineage, supporting their treatment in a distinct genus. An ENAS (Environmental Nucleic Acid Sequence) species, named *Haw. sequentia* ENAS, was also included in *Hawksworthiomyces* by De Beer *et al.* (2016). *Hawksworthiomyces* species have been isolated from diverse sources (*e.g.* *Eucalyptus* wood poles, insect fungal gardens, rhizospheres of plants) in South Africa, North and Central America, South Korea and Europe (De Beer *et al.* 2016). In the analyses of our datasets based on protein coding genes (Figs S3, S4) *Hawksworthiomyces* spp. formed two separate lineages. However, in the concatenated (Fig. 5) and LSU (Fig. S1) datasets, a monophyletic lineage emerged.

## Heinzbutinia (Lineage XXIV)

**Heinzbutinia** Z.W. de Beer & M. Procter, *gen. nov.* MycoBank MB 840404. Fig. 9A, B.

*Etymology*: Named for Prof. Heinz Butin (1928–2021), a German forest pathologist who described 10 new species in the *Ophiostomatales* between 1968 and 1990, including the type species of this novel genus.

*Sexual morph*: *Ascomatal bases* black, subglobose to globose; necks black, cylindrical, curved. *Ostiolar hyphae* absent. *Asci* elongate ovoid or clavate, evanescent. *Ascospores* hyaline, 1-celled, orange segment-like in side view, ellipsoidal in face view.

*Asexual morph*: Sporothrix-like; *conidiophores* micronematous, macronematous, mononematous, simple or branched, hyaline; *conidiogenous cells* sympodial, denticulate; *conidia* hyaline, 1-celled, ellipsoid, often curved, reniform, secondary conidia originating from swollen ellipsoidal conidia, oblong, straight or curved.

*Type species*: *Heinzbutinia grandicarpa* (Kowalski & Butin) Z.W. de Beer & M. Procter, *comb. nov.* MycoBank MB 840405.

*Basionym*: *Ceratocystis grandicarpa* Kowalski & Butin, J. Phytopathol. 124: 243. 1989. MycoBank MB 134497.

*Synonym*: *Ophiostoma grandicarpum* [as '*grandicarpa*'] (Kowalski & Butin) Rulamort, Bull. Soc. Bot. Centre-Ouest 21: 511. 1990. MycoBank MB 130251.

*Phylogenetic data*: Villarreal *et al.* (2005), De Beer & Wingfield (2013), Reid & Hausner (2015), De Beer *et al.* (2016a, b), De Errasti *et al.* (2018).

*Notes*: The *O. grandicarpum* complex was described by De Beer *et al.* (2016b) for the monophyletic lineage formed by *O. grandicarpum* and *O. microsporum* among other genera in the *Ophiostomatales* (De Beer & Wingfield 2013, Reid & Hausner 2015, De Beer *et al.* 2016a, De Errasti *et al.* 2018). In our expanded phylogenies, the two species again consistently formed a well-supported lineage distinct from all other genera in the *Ophiostomatales* (Figs 5, S2–S4). Both species are characterised by very long (more than 1 mm) ascomatal necks (Kowalski & Butin 1989, Hunt 1956), sporothrix-like asexual morphs and reniform ascospores (Fig. 3F; Type A as categorised by De Beer & Wingfield 2013). Both species were isolated from hardwoods. Based on the distinct phylogenetic placement and supported by a unique morphology and ecology, we have designated the *O. grandicarpum* complex as the new genus *Heinzbutinia*.

### Other new combinations:

**1) *Heinzbutinia microspora*** (Arx) Z.W. de Beer & M. Procter, *comb. nov.* MycoBank MB 840406.

*Basionym*: *Ophiostoma microsporum* Arx, Antonie van Leeuwenhoek 18: 211. 1952. MycoBank MB 302079.

*Synonyms*: *Ceratostomella microspora* R.W. Davidson, Mycologia 34: 650. 1942. MycoBank MB 284860. *nom. illegit.*, Art. 53.1, later homonym for *Cs. microspora* Ellis & Everh., see De Beer *et al.* 2013, Section C.1.

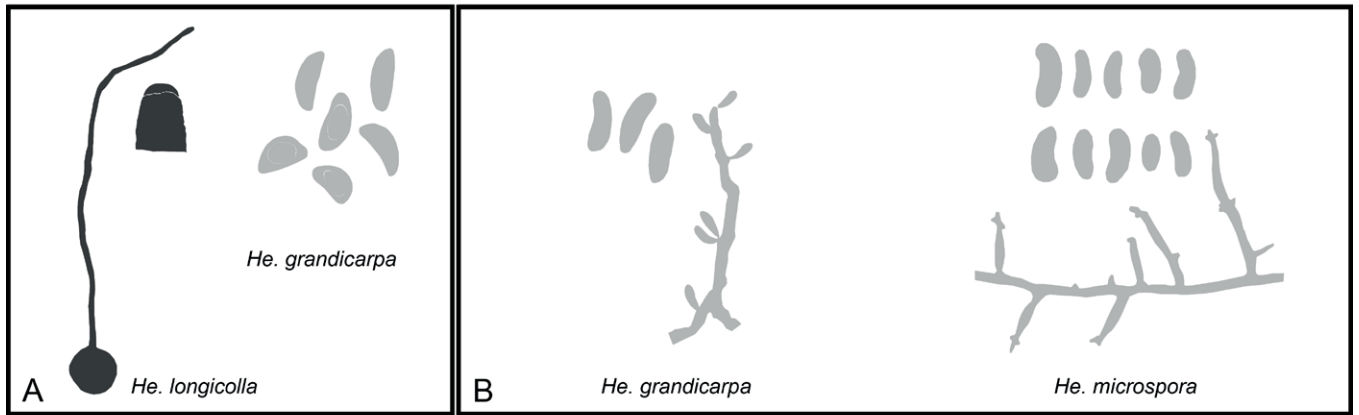
*Ceratocystis perparvispora* J. Hunt, Lloydia 19: 46. 1956. MycoBank MB 294227. Art. 52.1, superfluous *nom. nov.*

*Ceratocystis microspora* (R.W. Davidson) R.W. Davidson & Aoshima, Ph.D. thesis, University of Tokyo: 20. 1965. *nom. inval.*, Arts 29.1, 39.1 or 39.2.

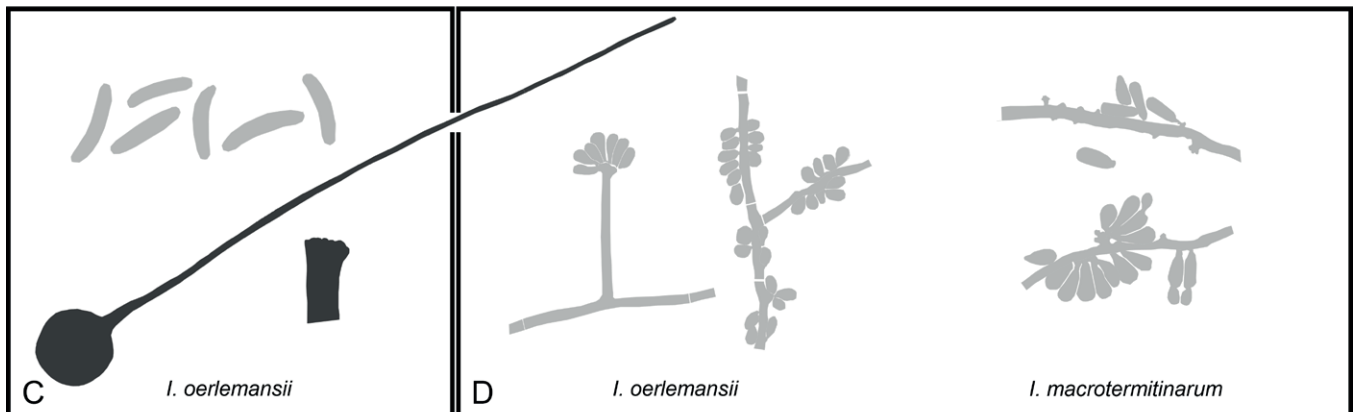
*Ceratocystis microspora* (Arx) R.W. Davidson, J. Colorado-Wyoming Acad. Sci. 6: 16. 1969. MycoBank MB 453851.

*Descriptions*: Hunt (1956: 46–47), Griffin (1968: 710), De Hoog (1974: 63–64, fig. 25), Olchoweki & Reid (1974: 1709), Upadhyay (1981: 50, figs 104–108), Maekawa *et al.* (1987: 8, 10, figs 1–6).

*Heinzbutinia*



*Intubia*



*Jamesreidia*

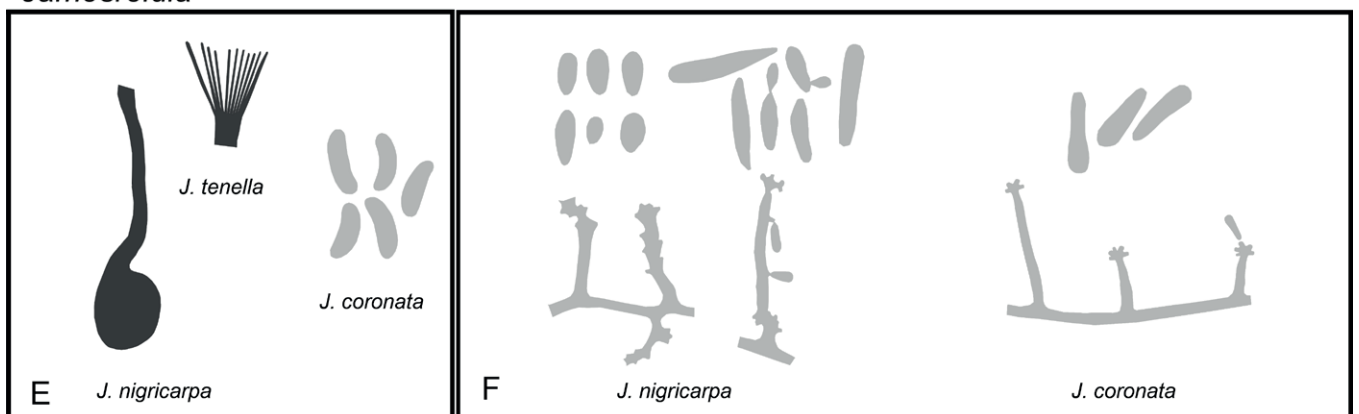


Fig. 9. Genera of the *Ophiostomatales* redrawn from published images with sexual morphs (if known) on the left and asexual morphs on the right. A, B. *Heinzbutinia*. C, D. *Intubia*. E, F. *Jamesreidia*. (Pale grey shading reflects hyaline to subhyaline colouration, medium-tone grey brown to dark brown and dark grey reflects fuscous black to dark black colouration).

*Phylogenetic data:* Hausner *et al.* (1993b), Mullineux *et al.* (2011), De Beer & Wingfield (2013), Musvuugwa *et al.* (2015), De Beer *et al.* (2016a, b).

*Notes:* This species grouped with *He. grandicarpa* and distinct from other *Ophiostoma* spp. (De Beer *et al.* 2016a, b), in the *O. grandicarpum* complex as designated by De Beer *et al.* (2016b). See note under *He. grandicarpa*. The name *He. microspora* should not be confused with *Leptographium microsporum* or *Ceratostomella microspora* (see De Beer *et al.* 2013, section C.2).

**2) *Heinzbutinia solheimii*** (Strzalka & Jankowiak) Z.W. de Beer & M. Procter, **comb. nov.** MycoBank MB 840407.

*Basionym:* *Ophiostoma solheimii* Strzalka & Jankowiak, Antonie van Leeuwenhoek 112: 1517. 2019. MycoBank MB 830198.

*Description:* Jankowiak *et al.* (2019: 1516–1517, fig. 8).

*Phylogenetic data:* Jankowiak *et al.* (2019).

*Notes:* This species is closely related to and formed a well-supported lineage with *He. grandicarpa* and *He. microspora* (Jankowiak *et al.* 2019, figs 1, S4).

***Intubia***

***Intubia*** W.J. Nel *et al.*, Mycologia 113: 1206. 2021. MycoBank MB 837565. Fig. 9C, D.

*Etymology:* 'From the Xhosa language, Intubi for termite, recognising the source where the fungus was found' (Nel *et al.* 2021).

*Sexual morph:* Ascum bases dark brown, globose; necks uniformly dark, often slightly curved, tapering towards apex, extremely long. *Ostiolar hyphae* absent. *Asci* not seen. *Ascospores* produced in slimy droplet at apex of neck, hyaline, 1-celled, cylindrical, sometimes slightly curved, no sheath.

*Asexual morph:* *Conidiophores* micronematous, hyaline, arising singly. Hyalorhinocladia-like; *conidiogenous cells* smooth; *conidia* hyaline, 1-celled, bacilliform tapering toward one end, occasionally producing secondary spores. Sporothrix-like; *conidiogenous cells* denticulate; *conidia* of two types, first type formed on vegetative hyphae, hyaline, 1-celled, round to obovoid, second type formed on conidiophores, hyaline, 1-celled, bacilliform, secondary conidia present.

*Type species:* *Intubia macrotermittinarum* W.J. Nel et al., Mycologia 113: 1208. 2021. MycoBank MB 837567.

*Other species:* Listed in Table 1.

*Notes:* Distinguished from other phylogenetically related genera in the *Ophiostomatales* for their unique habitat with dark coloured ascumata embedded in the substrate of abandoned *Termitomyces* combs.

## Jamesreidia (Lineage XII)

*Jamesreidia* Z.W. de Beer & M. Procter, **gen. nov.** MycoBank MB 840408. Fig. 9E, F.

*Etymology:* Named for the Canadian mycologist, Dr James Reid, who described 28 novel ophiostomatoid species, including the type species of this new genus. He was also involved in producing some of the first phylogenetic data based on ribosomal sequences distinguishing between the *Ophiostomatales* and *Microascales* (Olchowecki & Reid 1974, Hausner et al. 1992).

*Synonym:* *Ophiostoma tenellum* complex *sensu* Z.W. de Beer & M.J. Wingf., In *The Ophiostomatoid Fungi: Expanding Frontiers*: 34. 2013.

*Sexual morph:* Ascum bases black, globose; necks absent or present, black, straight or bent. *Ostiolar hyphae* divergent. *Asci* evanescent, clavate to subglobose. *Ascospores* hyaline, 1-celled, orange segment-like in side view, oblong in face view, broadly ellipsoidal to globose in end view.

*Asexual morph:* *Conidiophores* macronematous, semimacronematous, mononematous, hyaline, simple or branched. *Conidiogenous cells* polyblastic, denticulate. *Conidia* hyaline, 1-celled, broadly ovoid to nearly cylindrical, slightly curved.

*Type species:* *Jamesreidia tenella* (R.W. Davidson) Z.W. de Beer & M. Procter, **comb. nov.** MycoBank MB 840409.

*Basionym:* *Ceratocystis tenella* R.W. Davidson, Mycologia 50: 666. 1958. MycoBank MB 294240.

*Synonyms:* *Ophiostoma tenellum* (R.W. Davidson) M. Villarreal, Mycotaxon 92: 263. 2005. MycoBank MB 346181.

*Ceratocystis capitata* H.D. Griffin, Canad. J. Bot. 46: 699. 1968. MycoBank MB 327623.

*Descriptions:* Griffin (1968: 713, 715, fig. 93, pl. III), Olchowecki & Reid (1974: 1708, pl. XVI figs 307, 308, 311, 312), Upadhyay

(1981: 114, figs 408–412), Maekawa et al. (1987: 10–11, figs 19, 20), Hutchison & Reid (1988a: 68).

*Phylogenetic data:* Villarreal et al. (2005), Linnakoski et al. (2010, 2016), De Beer & Wingfield (2013), De Errasti et al. (2018), De Beer et al. (2016a), De Errasti et al. (2018), Wang et al. (2018), Chang et al. (2019).

*Notes on the type species:* *Jamesreidia tenella* groups with *J. coronata*, *J. nigricarpa* (Fig. 5; Linnakoski et al. 2010, De Beer & Wingfield 2013) and *J. rostrocoronata* (in the phylogenies of De Beer et al. 2016a) to form *Jamesreidia*, previously designated as the *O. tenellum* species complex (De Beer & Wingfield 2013). This species serves as the type species of the new genus, due to the fact that it is the oldest described species in the genus.

*Notes on the genus:* The *O. tenellum* complex was defined in *Ophiostoma s.l.* by De Beer & Wingfield (2013), who noted that members of the complex shared a similar morphology with species in the *S. schenckii*-*O. stenoceras* complex (also treated in *Ophiostoma s.l.* at the time, but now recognised as the genus *Sporothrix*). The asexual morphs of all species can be described as sporothrix-like and sexual morphs form Type A ascospores (Fig. 3F; as categorised by De Beer & Wingfield 2013). All species in this complex colonise conifer wood in North America (Linnakoski et al. 2010).

De Beer et al. (2016a) noted that the generic status of the *O. tenellum* complex should be further investigated, because it grouped distinctly from both *Sporothrix* and *Ophiostoma s.s.* in their phylogenies. In the present study, this complex grouped separately from what we have designated as *Ophiostoma* and *Sporothrix* in our phylogeny (Fig. 5) as well as in the phylogenies of other authors (Villarreal et al. 2005, Linnakoski et al. 2010, De Beer & Wingfield 2013, De Beer et al. 2016a). We have thus elevated the status of the *O. tenellum* complex to that of a genus, for which we have provided the name *Jamesreidia*.

### Other new combinations:

**1) *Jamesreidia coronata*** (Olchow. & J. Reid) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840410.

*Basionym:* *Ceratocystis coronata* Olchow. & J. Reid, Canad. J. Bot. 52: 1705. 1974. MycoBank MB 310490.

*Synonym:* *Ophiostoma coronatum* (Olchow. & J. Reid) M. Villarreal, Mycotaxon 92: 263. 2005. MycoBank MB 346368.

*Description:* Hutchison & Reid (1988a: 66, 68).

*Phylogenetic data:* Hausner et al. (1993b), Thwaites et al. (2005), Villarreal et al. (2005), Linnakoski et al. (2010), Mullineux et al. (2011), De Beer & Wingfield (2013), Linnakoski et al. (2016), De Beer et al. (2016a), De Errasti et al. (2018), Wang et al. (2018), Chang et al. (2019).

*Notes:* This species grouped in *Jamesreidia* (Fig. 5), previously designated as the *O. tenellum* species complex (De Beer & Wingfield 2013).

**2) *Jamesreidia nigrocarpa*** (R.W. Davidson) M. Procter & Z.W. de Beer, **comb. nov.** [MycoBank MB 840411]

*Basionym:* *Ceratocystis nigrocarpa* R.W. Davidson, Mycopathol. Mycol. Appl. 28: 276. 1966. MycoBank MB 327637.



*Synonym:* *Ophiostoma nigrocarpum* (R.W. Davidson) de Hoog, Stud. Mycol. 7: 62. 1974. MycoBank MB 319024.

*Descriptions:* De Hoog (1974: 62–63, fig. 24), Olchowecki & Reid (1974: 1709), Upadhyay (1981: 104, figs 378–381), Benade *et al.* (1997: 1110–1111, figs 6–11).

*Phylogenetic data:* Aghayeva *et al.* (2004), Zhou *et al.* (2004a, 2006), Roets *et al.* (2006, 2008, 2010), Zipfel *et al.* (2006), De Meyer *et al.* (2008), Linnakoski *et al.* (2010), Madrid *et al.* (2010), Romón *et al.* (2014b), De Errasti *et al.* (2016, 2018), Linnakoski *et al.* (2016), De Beer *et al.* (2016a), Giraldo *et al.* (2017), Chang *et al.* (2019).

*Notes:* This species forms part of *Jamesreidia* (Fig. 5), previously the *O. tenellum* species complex (De Beer & Wingfield 2013).

**3) *Jamesreidia rostrocoronata*** (R.W. Davidson & Eslin) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840412.

*Basionym:* *Ceratocystis rostrocoronata* R.W. Davidson & Eslin, Mem. N.Y. Bot. Gard. 28: 50. 1976. MycoBank MB 310518.

*Synonym:* *Ophiostoma rostrocoronatum* (R.W. Davidson & Eslin) de Hoog & R.J. Scheff., Mycologia 76: 297. 1984. MycoBank MB 107077.

*Descriptions:* Upadhyay (1981: 112), Hutchison & Reid (1988a: 76–78).

*Phylogenetic data:* Hausner *et al.* (1993b), Jacobs *et al.* (2003), Villarreal *et al.* (2005), Linnakoski *et al.* (2010), De Beer & Wingfield (2013), Reid & Hausner (2015), De Beer *et al.* (2016b), Osorio *et al.* (2016), Jankowiak *et al.* (2017b), Wang *et al.* (2018).

*Notes:* A LSU sequence generated by Jacobs *et al.* (2003) was shown to group in *Sporothrix* (De Beer & Wingfield 2013, Osorio *et al.* 2016, Jankowiak *et al.* 2017, Wang *et al.* 2018). However, sequence data generated by De Beer *et al.* (2016b) for the same isolate, placed *O. rostrocoronatum* with the *O. tenellum* complex. Based on analyses of sequences from four gene regions and morphological characteristics, De Beer *et al.* (2016b) proceeded to treat *O. rostrocoronatum* in the *O. tenellum* complex. We have consequently treated this species as part of the lineage described here as *Jamesreidia*.

## ***Leptographium* (Lineage I)**

***Leptographium*** Lagerb. & Melin, Svenska Skogsv.-Fören. Tidskr. 25: 257. 1927. MycoBank MB 8749, **emend.** Z.W. de Beer & M. Procter. Figs 10, 11.

*Etymology:* ‘A thin, small brush. From the Greek adjective, λεπτός (thin) and the Greek noun γραφίον (a small brush). The generic name refers to the conidiophores that resemble small brushes’ (Jacobs & Wingfield 2001).

*Synonyms:* *Scopularia* Preuss, Linnaea 24: 133. 1851. MycoBank MB 22345, *nom. illegit.*, Art. 53.1. (Type species *Sc. venusta* Preuss).

*Phialographium* H.P. Upadhyay & W.B. Kendr., Mycologia 66: 183. 1974. MycoBank MB 9340. (Type species *Ph. sagmatosporae* H.P. Upadhyay & W.B. Kendr.).

*Graphiocladiella* H.P. Upadhyay, A Monograph of *Ceratocystis* and

*Ceratocystiopsis*: 138. 1981. MycoBank MB 8394. (Type species *G. clavigera* H.P. Upadhyay).

?= *Europhium* A.K. Parker, Canad. J. Bot. 35: 175. 1957. MycoBank MB 1938. [Type species *E. trinacriforme* A.K. Parker; Placement uncertain, see De Beer *et al.* (2013b)].

*Sexual morph:* *Ascomata* cleitothecial or perithecial; bases black, subglobose to globose; necks absent or present, very short, elongated, cylindrical, straight or flexuous. *Ostiolar hyphae* absent. *Asci* evanescent, clavate to broadly clavate. *Ascospores* hyaline, 1-celled, enclosed in sheath, reniform or cucullate in side view, oblong or rectangular in face view, ovoid, globose or triangular in end view.

*Asexual morph:* *Conidiophores* macronematous, micronematous, mononematous, singly or in groups, upright or prone, branches brown, becoming paler towards upper branches, bases simple or rhizoid-like. *Conidiogenous cells* hyaline, cylindrical. *Conidia* hyaline, 1-celled, oblong, pyriform, broadly ellipsoidal to obovoid, with truncate base. Hyalorhinocliadiella-like; *conidiophores* simple or branched, upright; *conidia* hyaline, 1-celled, oblong to ellipsoid. Pesotum-like; *conidiophores* pale to dark brown, hyaline to light grey, reddish brown at apex; *conidia* hyaline, 0–4-celled, oblong, cylindrical to clavate, broadly fusiform, or subglobose to ellipsoid with truncate base. *Ramoconidia* hyaline, clavate to ellipsoid, 1-celled spores. Serpentine hyphae present in *L. lundbergii*, *L. serpens* complexes and *L. douglasii* in *L. wagneri* complex.

*Type species:* *Leptographium lundbergii* Lagerb. & Melin, Svenska Skogsv.-Fören. Tidskr. 25: 248. 1927. MycoBank MB 269891.

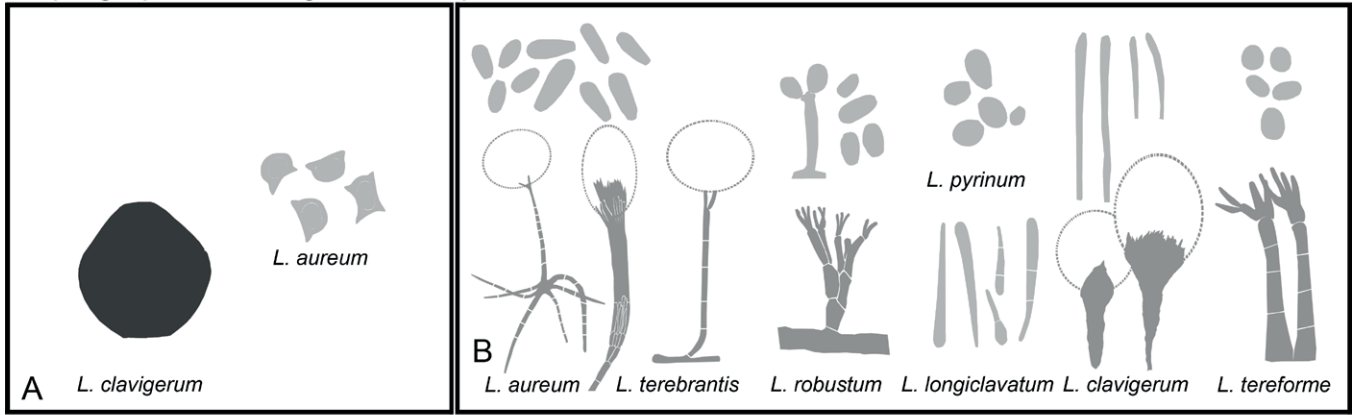
*Synonym:* *Scopularia lundbergii* (Lagerb. & Melin) Goid., Ann. Mycol. 31: 138. 1933. MycoBank MB 253103.

*Notes on the genus:* *Leptographium* was originally described as an asexual genus with *L. lundbergii* as type species (Lagerberg *et al.* 1927). Soon afterwards, the sexual genus *Grosmannia* was described to accommodate the sexual morph of another species, *Leptographium penicillatum* (Goidànich 1935). During the course of the next 65 years, an additional 28 asexual species were described in *Leptographium* and 17 species with known sexual morphs that were treated in different genera (Harrington 1988, Wingfield 1993). This prompted a revision of the genus in a comprehensive monograph by Jacobs & Wingfield (2001), who treated the sexual morphs of these species in *Ophiostoma*, of which *Grosmannia* was listed as one of several synonyms (Jacobs & Wingfield 2001). As mentioned in the introduction to this study, Zipfel *et al.* (2006) reinstated *Grosmannia* for all sexual species with *Leptographium* asexual morphs. However, they included only one asexual species, *L. lundbergii*, in their phylogeny.

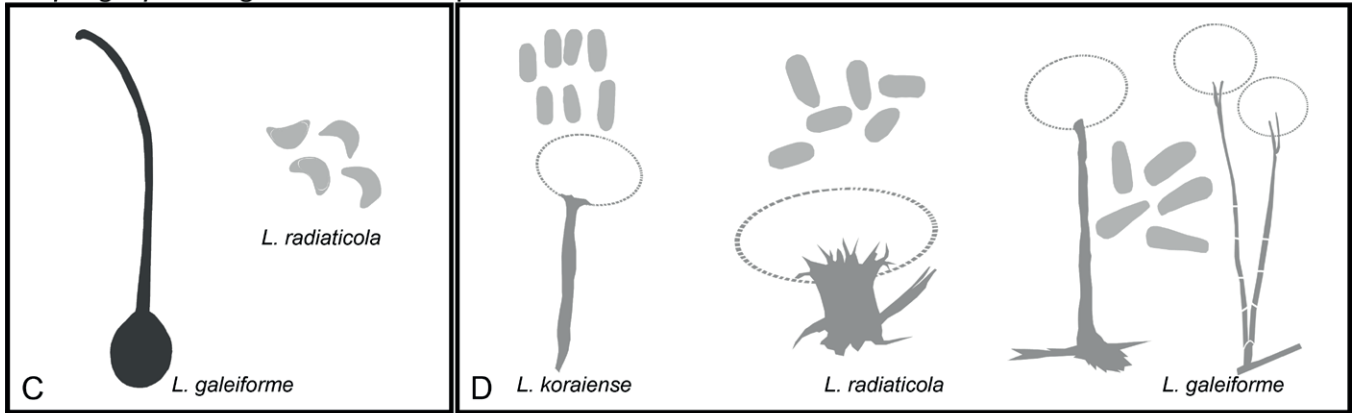
De Beer & Wingfield (2013) were the first authors to apply the One Fungus-One Name principles to the *Ophiostomatales*, and listed *Grosmannia* as synonym of the older name, *Leptographium*. However, they recognised that the type species for these two genera grouped in different lineages but concluded that their LSU and ITS phylogenies were not sufficiently robust to resolve the generic status of these sub-lineages within what they referred to as ‘*Leptographium sensu lato*’. They listed 94 valid species in this broad concept but refrained from making new combinations for species that did not have names in *Leptographium*, recommending that phylogenies based on a greater number of gene regions should be used to resolve the genera.

Prior to the study of De Beer & Wingfield (2013), several authors defined phylogenetic species complexes in ‘*Leptographium sensu*

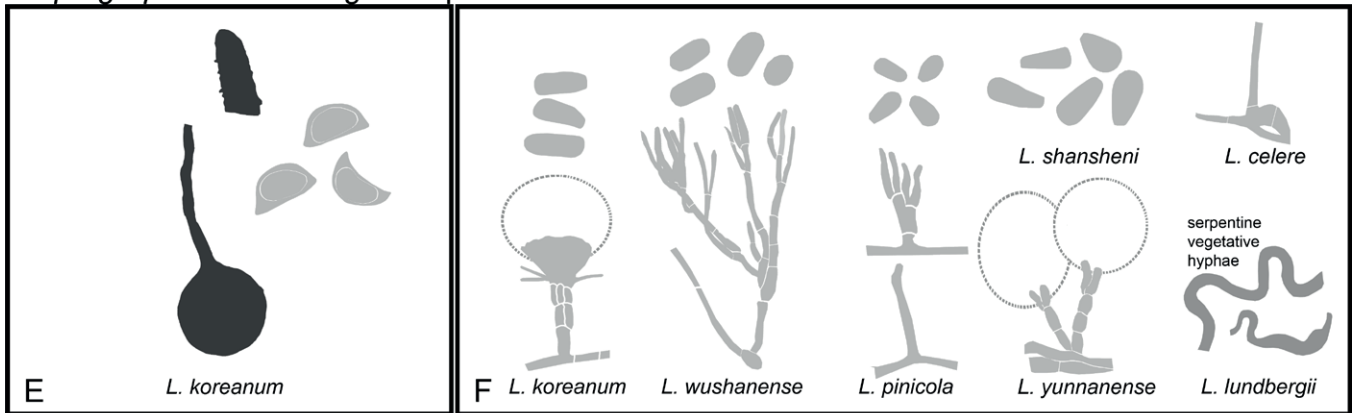
*Leptographium clavigerum* complex



*Leptographium galeiforme* complex



*Leptographium lundbergii* complex



*Leptographium olivaceum* complex

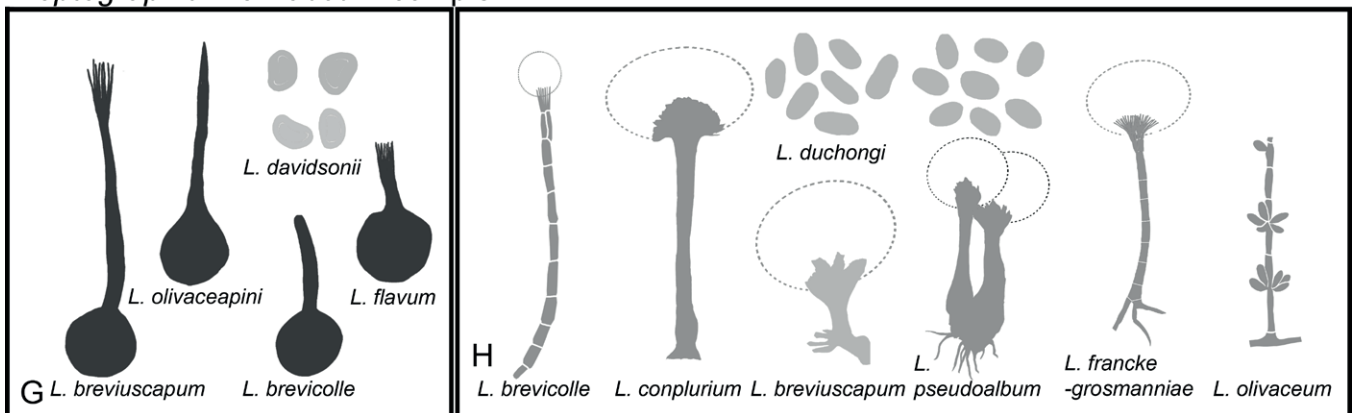
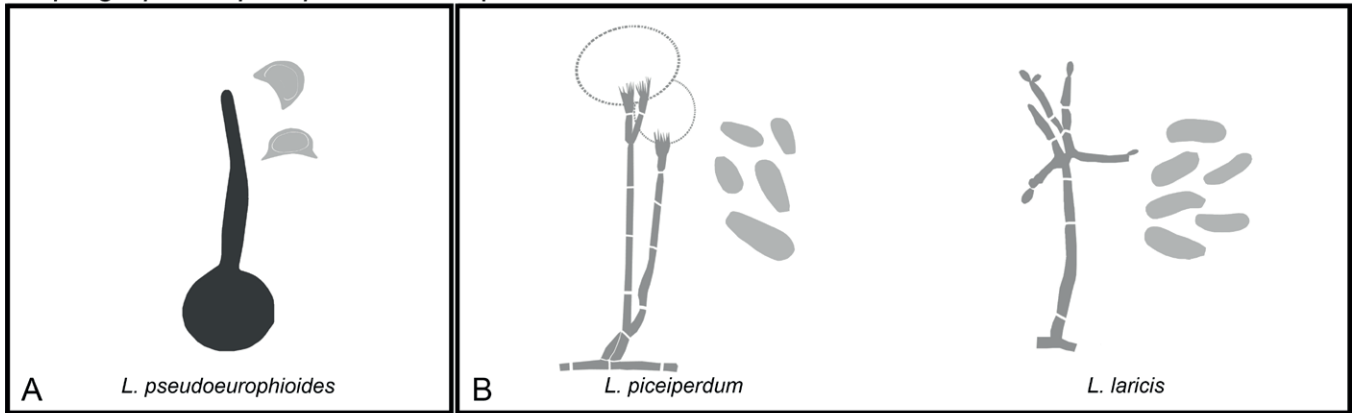
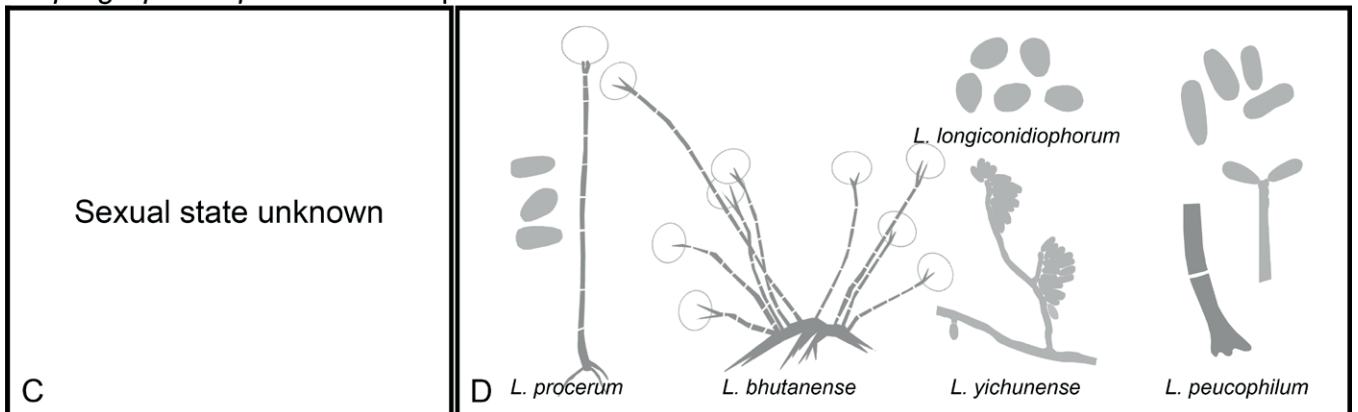


Fig. 10. Genera of the *Ophiostomatales* redrawn from published images with sexual morphs (if known) on the left and asexual morphs on the right. A, B. *Leptographium clavigerum* complex. C, D. *Leptographium galeiforme* complex. E, F. *Leptographium lundbergii* complex. G, H. *Leptographium olivaceum* complex. (Pale grey shading reflects hyaline to subhyaline colouration, medium-tone grey brown to dark brown and dark grey reflects fuscous black to dark black colouration).

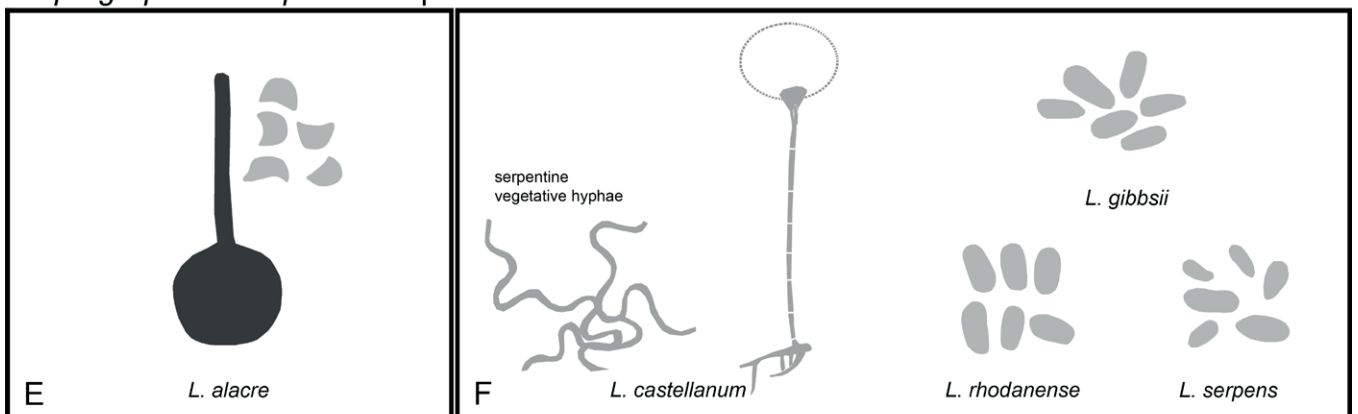
*Leptographium piceiperdum* complex



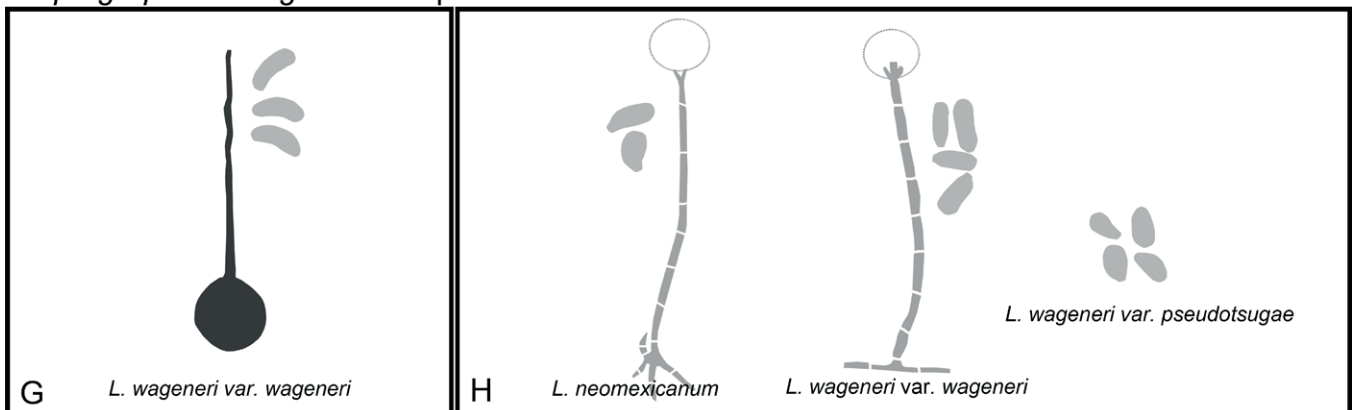
*Leptographium procerum* complex



*Leptographium serpens* complex



*Leptographium wagneri* complex



**Fig. 11.** Genera of the *Ophiostomatales* redrawn from published images with sexual morphs (if known) on the left and asexual morphs on the right. **A, B.** *Leptographium piceiperdum* complex. **C, D.** *Leptographium procerum* complex. **E, F.** *Leptographium serpens* complex. **G, H.** *Leptographium wagneri* complex. (Pale grey shading reflects hyaline to subhyaline colouration, medium-tone grey brown to dark brown and dark grey reflects fuscous black to dark black colouration).

*lato*' (Massoumi Alamouti *et al.* 2011, Six *et al.* 2011, Duong *et al.* 2012, Linnakoski *et al.* 2012). The results of the present study clearly show that '*Leptographium sensu lato*' represents two distinct genera. These include *Leptographium* (Lineage I) with *L. lundbergii* as type species and including eight species complexes defined below and *Grosmannia* (Lineage II) defined by *G. penicillata* including two species complexes defined above. A third complex could emerge as new species are described in *Grosmannia*.

The last formal morphological description of *Leptographium* was provided by Jacobs & Wingfield (2001) for asexual fungi forming mononematous conidiophores and branched conidiogenous apparatuses. In view of the One Fungus-One Name principles, we have emended the description of *Leptographium* to accommodate the morphology of the sexual morphs, treated previously in *Grosmannia*, *Ophiostoma*, *Ceratocystis* or *Europhium* (Upadhyay 1981, Jacobs & Wingfield 2001, De Beer & Wingfield 2013). Morphology of synnematos asexual morphs previously excluded from *Leptographium* and treated variously as species of *Graphium*, *Pesotum*, *Phialographium* or *Graphiocladiella* (Upadhyay & Kendrick 1974, Upadhyay 1981, Seifert & Okada 1993, Okada *et al.* 1998) have also been incorporated in the revised circumscription of the genus.

### Species complexes:

#### The *L. clavigerum* complex

The *L. clavigerum* complex was first described by Massoumi Alamouti *et al.* (2011) as the *G. clavigera* complex. *Grosmannia clavigera* is also the type species of *Graphiocladiella*, a genus originally described for the asexual morphs of '*Ceratocystis*' species forming mononematous and synnematos conidiophores (Upadhyay 1981, Harrington 1988). Harrington (1988) proceeded to reduce *Graphiocladiella* to synonymy with *Graphium* (in which he also included species producing leptographium-like conidiophores). Species in the *G. clavigera* complex produce mostly synnematos aggregates of leptographium-like conidiophores, cleistothecal ascomata and reniform ascospores with hat-shaped sheaths (Linnakoski *et al.* 2012, De Beer & Wingfield 2013).

The first whole genome sequence produced for species in the *Ophiostomatales* was that for *G. clavigera*. This work was justified by the close association of *G. clavigera* with the mountain pine beetle (*Dendroctonus ponderosae*), a native but invasive pest causing devastating losses in the Northwestern USA and Canada (Kim *et al.* 2004, Massoumi Alamouti *et al.* 2011, De Beer & Wingfield 2013). Genome data were then used to show that what was previously thought to be a highly variable population of *G. clavigera*, actually represents a complex including multiple species (Massoumi Alamouti *et al.* 2011). Later studies contributed additional species to this new species complex (Six *et al.* 2011, De Beer & Wingfield 2013). In the present study, the *G. clavigera* complex formed a well-supported monophyletic lineage, and currently includes eight well-defined species, as well as one undescribed species (Massoumi Alamouti *et al.* 2011).

#### The *L. galeiforme* complex

The *L. galeiforme* complex was first described as the *O. galeiformis* complex when Zhou *et al.* (2004b) designated an epitype for the species (Bakshi 1951). Kim *et al.* (2005b) showed that *G. radiaticola* was part of the complex, and that this species was conspecific with the asexual species, *Hyalopesotum pini*. The latter species name was thus used for the asexual morph of *G. radiaticola* (Kim *et al.* 2005b, De Beer & Wingfield 2013). However, when the One Fungus–One Name principles are applied, the oldest

epithet '*pini*' (Hutchison & Reid 1988b) should take precedence over '*radiaticola*' (Kim *et al.* 2005b). We have consequently provided a new combination, *L. pini*, to represent this species. It was previously believed that *G. radiaticola* and *G. galeiformis* were the same species (Thwaites *et al.* 2005). However, data from the studies of Kim *et al.* (2005b) and Linnakoski *et al.* (2012) showed that these are distinct species, and that in addition to these, the complex includes two as yet undescribed cryptic species. Chang *et al.* (2017) reported *L. pini* (as *G. radiaticola*) from China, as well as another possible new species in the complex.

All species in the *L. galeiforme* complex produce synnemata that appear to be loose aggregates of leptographium-like conidiophores (Zhou *et al.* 2004b, Linnakoski *et al.* 2012, De Beer & Wingfield 2013). The distinction between the two species is also supported by the ecology of these fungi, with *L. galeiforme* being associated with conifer-infesting bark beetles in Europe, and *L. pini* (as *G. radiaticola*) associated with pine-infesting bark beetles with a wider distribution (South Africa, Chile, Europe, China, Korea, and New Zealand; Linnakoski *et al.* 2012).

#### The *L. lundbergii* complex

The *L. lundbergii* complex was first defined by Jacobs *et al.* (2005). In a study emerging from a survey of ophiostomatoid fungi in Finland and Russia, Linnakoski *et al.* (2012) expanded the complex to include additional species that group close to *L. lundbergii*. Although these species always grouped close together, they never formed a well-supported monophyletic lineage, neither in the analyses of Linnakoski *et al.* (2012), various subsequent analyses (De Beer & Wingfield 2013, Jankowiak *et al.* 2017, 2018, Chang *et al.* 2017, Pan *et al.* 2020) nor those in the present study. However, for the sake of convenience, we have chosen to treat these species as a group. All the species produce relatively short conidiophores that have conidia with truncate bases, and the two sexually reproducing species produce cucullate ascospores (Linnakoski *et al.* 2012, De Beer & Wingfield 2013). Most of the species in this complex have been described from conifers in Asia and they have also been found in Europe, Canada, South Africa and New Zealand as the causal agents of sapstain in lumber (Linnakoski *et al.* 2012).

#### The *L. olivaceum* complex

The *L. olivaceum* complex accommodates species that are characterised by brownish synnematos asexual morphs and cucullate ascospores produced in ascomata with almost cylindrical necks and prominent ostiolar hyphae (Yin *et al.* 2019). The complex was first demarcated in a phylogeny by Six *et al.* (2011), more comprehensively defined by Linnakoski *et al.* (2012), and subsequently recognised by De Beer & Wingfield (2013) and Jankowiak *et al.* (2017, 2018). The complex includes *L. sagmatosporum*, the type species of the genus *Phialographium* (Upadhyay & Kendrick 1974), and its inclusion in the complex renders that name a synonym of *Leptographium* (De Beer & Wingfield 2013).

Most recently, Yin *et al.* (2019) added six new species to the complex. All species in this complex are associated with various bark beetles, mostly infesting spruce and pine trees in North America and Eurasia (Linnakoski *et al.* 2012, Jankowiak *et al.* 2017, 2018, Yin *et al.* 2019). The only exception is *L. francke-grosmanniae* that groups peripheral to the complex, has a morphology quite distinct from other species and was isolated from a bark beetle gallery on oak trees in Europe (Davidson 1971, Mouton *et al.* 1992, Yin *et al.* 2019). It is possible that this species represents a distinct species complex that cannot be distinguished at the present time.

### The *L. piceiperdum* complex

Linnakoski *et al.* (2012) first defined this species complex when they showed that isolates described as *G. piceiperda* separated into five distinct species, two of which were unnamed. Ando *et al.* (2016) focused on isolates from different sources in Japan, revealing several additional cryptic species. Both Linnakoski *et al.* (2012) and Ando *et al.* (2016) concluded that epitypification is needed for *L. piceiperdum* and *L. europhioides* in order to confirm the placement of these species, because sequences for them were derived from herbarium type material. All members of this complex form typical leptographium-like asexual morphs, have cucullate ascospores (De Beer & Wingfield 2013, Ando *et al.* 2016), and have been found in association with conifer infesting bark beetles (mostly *Ips* species) in Europe, North America, Russia and Japan (Linnakoski *et al.* 2012, Ando *et al.* 2016).

### The *L. procerum* complex

The *L. procerum* complex was first defined by De Beer & Wingfield (2013), and studied by Yin *et al.* (2015). These authors used seven gene regions to evaluate the species boundaries in the complex, and showed that it accommodates nine species. No sexual morph has been observed for any species in this complex, and asexual morphs can be described as leptographium-like (Jacobs *et al.* 2000b, 2006, Jacobs & Wingfield 2001, Lu *et al.* 2008, Paciura *et al.* 2010, De Beer & Wingfield 2013, Yin *et al.* 2015). Species in this complex are associated with conifer-infesting bark beetles in North America and Eurasia, with most described from East Asia. The exception is *L. profanum* that occurs on hardwood trees in the USA (Linnakoski *et al.* 2012, Yin *et al.* 2015). Most species in this complex are not widely distributed, with single species being found only in single countries. However, *L. procerum* has been isolated from *Pinus* spp. in China, Russia and the USA (Yin *et al.* 2015).

The *L. procerum* complex has received considerable attention by researchers. This is due to the fact that *L. procerum*, the type species of the complex has been associated with a root and root-collar disease of *Pinus* spp. in the USA known as white pine root decline (Kendrick 1962, Dochinger 1967, Wingfield 1983, Wingfield *et al.* 1994). Furthermore, *L. procerum* is associated with the red turpentine beetle (*Dendroctonus valens*), which is native to North America and possibly western Europe and was introduced into China resulting in devastating losses of Chinese native pines (Yan *et al.* 2005, Lu *et al.* 2008, Taerum *et al.* 2012, 2013, 2017, Zhou *et al.* 2013, Sun *et al.* 2013, Yin *et al.* 2015).

### The *L. serpens* complex

The *L. serpens* species complex was first recognised based on phylogenetic analyses by Six *et al.* (2011). In a focused study to resolve typification issues in the complex, Duong *et al.* (2012) showed that *L. serpens*, previously recognised as a single taxon represented five distinct species. All of these species produce typical leptographium-like conidiophores, with characteristic serpentine hyphae on agar, while ascospores produced by two of the species are sheathed (Wingfield & Marasas 1980, Jacobs & Wingfield 2001, Duong *et al.* 2012). Interestingly, most of the members of the complex have relatively narrow distributions, most being known from only a single country. For example, *L. serpens* occurs in Italy, *L. gibbsii* in the UK, *L. yamaoake* in Japan and *L. castellanum* in Spain and the Dominican Republic. The exception here is *L. alacre* that is more widely distributed and associated with conifer-root infesting bark beetles in South Africa and Italy (Duong *et al.* 2012), although its occurrence in South Africa is certainly due to an accidental introduction likely from Europe. Marinowitz *et al.*

(2017) described a morphologically similar species, *L. rhodanense* from Switzerland that groups between the *L. serpens* and the *L. wageneri* complexes.

### The *L. wageneri* complex

Six *et al.* (2011) first defined the *L. wageneri* species complex based on phylogenetic analyses. All species in this complex form typical leptographium-like asexual morphs. However, the sexual morph has been observed only for *L. wageneri* var. *ponderosae*, and this was described as *G. wageneri* (Goheen & Cobb 1978, Zipfel *et al.* 2006). This fungus produces allantoid ascospores, but unlike other *Leptographium* ascospores, no sheath was reported (Goheen & Cobb 1978, Jacobs & Wingfield 2001). Most of the species in the complex are associated with conifer-root infesting beetles in the USA (Cobb *et al.* 1974, 1984, Hansen *et al.* 1988, Witcosky & Hansen 1985, Witcosky *et al.* 1986). The only exception is *L. reconditum*, which was isolated from the roots of *Triticum* species in South Africa (Jooste 1978).

The *L. wageneri* complex includes three host-specific varieties that are important pathogens of conifers restricted to the western USA and causing black stain root disease (Cobb 1988, Hessburg & Hansen 2000). These three formally described varieties can be distinguished from each other based on their morphological characteristics and the host tree species that they infect (Harrington & Cobb 1984, 1987, Jacobs & Wingfield 2001). *Leptographium wageneri* var. *pseudotsugae* occurs on Douglas fir (*Pseudotsuga menziesii*), *L. wageneri* var. *ponderosae* on hard pines (*Pinus ponderosa*, *P. jeffreyi* and *P. contorta*), and *L. wageneri* var. *wageneri* on pinyon pines (*P. monophylla* and *P. edulis*). Phylogenetic analyses in this study support the lineage defined as the *G. wageneri* complex by De Beer & Wingfield (2013) and Six *et al.* (2011).

### Groups A & B

*Leptographium pineti* grouped singly in *Leptographium* and this is consistent with phylogenies emerging from other studies (Paciura *et al.* 2010, Six *et al.* 2011, Duong *et al.* 2012, De Beer & Wingfield 2013). Chang *et al.* (2017) described a new species from China, *L. ningerense* (not included in our data), which grouped with *L. pineti* in their datasets.

*Grosmannia cainii* formed a lineage distinct from others in *Leptographium* in our analyses (Fig. 5) and this was also seen in the phylogenies of De Beer & Wingfield (2013).

### New combinations:

**1) *Leptographium cainii*** (Olchow. & J. Reid) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840389.

*Basionym:* *Ceratocystis cainii* Olchow. & J. Reid, *Canad. J. Bot.* 52: 1697. 1974. MycoBank MB 310486.

*Synonyms:* *Ophiostoma cainii* (Olchow. & J. Reid) T.C. Harr., *Mycotaxon* 28: 41. 1987. MycoBank MB 128912.

*Grosmannia cainii* (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf., *Stud. Mycol.* 55: 89. 2006. MycoBank MB 500812.

*Descriptions:* Upadhyay (1981: 39, figs 43–47), Seifert & Okada (1993: 32, fig. 3D).

*Phylogenetic data:* Hausner *et al.* (2000), Masuya *et al.* (2004), Kim *et al.* (2005b), Six *et al.* (2011), Duong *et al.* (2012), De Beer & Wingfield (2013), Jankowiak *et al.* (2017, 2018), Liu *et al.* (2017), De Errasti *et al.* (2018), Chang *et al.* (2019).

Notes: *Leptographium cainii* groups alone and distinct from other species complexes in *Leptographium* in our data (Fig. 5). This is consistent with the data presented by De Beer & Wingfield (2013).

**2) *Leptographium europhioides*** (E.F. Wright & Cain) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840392.

*Basionym:* *Ceratocystis europhioides* E.F. Wright & Cain, *Canad. J. Bot.* 39: 1222. 1961. MycoBank MB 327627.

*Synonyms:* *Ophiostoma europhioides* (E.F. Wright & Cain) H. Solheim, *Nordic J. Bot.* 6: 203. 1986. MycoBank MB 102979.

*Grosmannia europhioides* (E.F. Wright & Cain) Zipfel, Z.W. de Beer & M.J. Wingf., *Stud. Mycol.* 55: 90. 2006. MycoBank MB 500818.

*Ceratocystis shikotsuensis* Aoshima, Ph. D. thesis, University of Tokyo: 10. 1965. *nom. inval.*, Arts 29.1, 39.1 or 39.2.

*Descriptions:* Davidson *et al.* (1967: 929–930), Griffin (1968: 709, 713), Olchowecki & Reid (1974: 1699, pl. XIII, figs 259–261), De Hoog & Scheffer (1984: 295, fig. 2), Yamaoka *et al.* (1997: 1221–1222), Jacobs *et al.* (1998: 290–291), Jacobs *et al.* (2000a: 239).

*Phylogenetic data:* Hausner *et al.* (1993b, 2000), Okada *et al.* (1998), Schroeder *et al.* (2001), Masuya *et al.* (2004), Greif *et al.* (2006), Mullineux & Hausner (2009), Matsuda *et al.* (2010), Paciura *et al.* (2010), Six *et al.* (2011), Linnakoski *et al.* (2012), De Beer & Wingfield (2013), Musvuugwa *et al.* (2015), Ando *et al.* (2016), Yamaoka (2017), De Errasti *et al.* (2018).

Notes: *Leptographium europhioides* groups in the *L. piceiperdum* complex (Fig. 5). De Beer & Wingfield (2013) noted that species such as *G. europhioides*, previously treated as synonyms of *G. piceiperda* based on morphology (Jacobs *et al.* 2000a, Jacobs & Wingfield 2001), were possibly distinct species (Linnakoski *et al.* 2012). Ando *et al.* (2016) investigated the phylogenetic relationships of Japanese isolates assigned to the *L. piceiperdum* complex and recognised 13 lineages within the complex. These included lineages representing *G. aenigmatica*, *G. laricis*, *G. piceiperda* group D and eight representing distinct, but undescribed species (Ando *et al.* 2016, Yamaoka 2017). Ando *et al.* (2016) concluded that although *L. piceiperdum* (as *G. piceiperda*) and *L. europhioides* (as *G. europhioides*) are valid species, epitypification is needed for both species to resolve the identity of the remaining undescribed taxa.

**3) *Leptographium galeiforme*** (B.K. Bakshi) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840393.

*Basionym:* *Ceratocystis galeiformis* Bakshi, *Mycol. Pap.* 35: 13. 1951. MycoBank MB 294208.

*Synonyms:* *Ophiostoma galeiforme* (B.K. Bakshi) Math.-Käärik, Meddeland. Statens Skogs-Forstningsinst. 43: 47. 1953. MycoBank MB 302075 (as 'galeiformis').

*Grosmannia galeiformis* (B.K. Bakshi) Zipfel, Z.W. de Beer & M.J. Wingf., *Stud. Mycol.* 55: 90. 2006. MycoBank MB 500820.

*Descriptions:* Mathiesen-Käärik (1953: 47–50), Hunt (1956: 33), Wingfield (1993: 48, fig. 8), Zhou *et al.* (2004b: 1309–1311, fig. 2).

*Phylogenetic data:* Hausner *et al.* (2000), Zhou *et al.* (2004b), Kim *et al.* (2005b, 2011), Thwaites *et al.* (2005), Greif *et al.* (2006), Zipfel *et al.* (2006), Lu *et al.* (2009), Mullineux & Hausner (2009), Harrington *et al.* (2010), Matsuda *et al.* (2010), Paciura *et al.* (2010), Six *et al.* (2011), Duong *et al.* (2012), Linnakoski *et al.* (2012), De Beer & Wingfield (2013), Taerum *et al.* (2013), Masuya *et al.*

(2013), Huang & Chen (2014), Wang *et al.* (2014), Musvuugwa *et al.* (2015), De Beer *et al.* (2016a, b), Chang *et al.* (2017, 2019), Wingfield *et al.* (2017), Jankowiak *et al.* (2017), Liu *et al.* (2017), De Errasti *et al.* (2018).

Notes: This species grouped with *L. radiaticola* and undescribed species (Linnakoski *et al.* 2012, De Beer & Wingfield 2013) to form the *L. galeiforme* species complex (Fig. 5). In the phylogenies of Chang *et al.* (2019), *L. koraiensis* grouped within this species complex. The latter species was not included in our analyses.

**4) *Leptographium pseudoeurophioides*** (Olchow. & J. Reid) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840413.

*Basionym:* *Ceratocystis pseudoeurophioides* Olchow. & J. Reid, *Canad. J. Bot.* 52: 1700. 1974. MycoBank MB 310514.

*Synonyms:* *Ophiostoma pseudoeurophioides* (Olchow. & J. Reid) Hausner *et al.*, *Canad. J. Bot.* 71: 1264. 1993. MycoBank MB 362667.

*Grosmannia pseudoeurophioides* (Olchow. & J. Reid) Zipfel *et al.*, *Stud. Mycol.* 55: 91. 2006. MycoBank MB 500826.

*Descriptions:* Olchowecki & Reid (1974: 1700, figs 219–229).

*Phylogenetic data:* Hausner *et al.* (1993b, 2000), Masuya *et al.* (2004), Mullineux & Hausner (2009), Mullineux *et al.* (2011), De Beer & Wingfield (2013), Musvuugwa *et al.* (2015), De Errasti *et al.* (2018).

Notes: *Leptographium pseudoeurophioides* was assigned to the *G. penicillata* complex (Hausner *et al.* 1993b, 2000). However, based on a short LSU sequence produced by Hausner *et al.* (1993b, 2000) and ascospore morphology, De Beer & Wingfield (2013) suggested that *L. pseudoeurophioides* should form part of the *L. piceiperdum* complex, and that additional collections and fresh material would be required to confirm its placement. For the present, we treat this species in *Leptographium*.

**5) *Leptographium radiaticola*** (J.J. Kim *et al.*) M. Procter & Z.W. de Beer **comb. nov.** [MycoBank MB 840396]

*Basionym:* *Ophiostoma radiaticola* J.J. Kim *et al.*, *Mycotaxon* 91: 486. 2005. MycoBank MB 500832.

*Synonyms:* *Grosmannia radiaticola* (J.J. Kim *et al.*) Z.W. de Beer & M.J. Wingf., *Stud. Mycol.* 55: 91. 2006. MycoBank MB 500827.

*Hyalopesotum pini* L.J. Hutchison & J. Reid, *New Zealand J. Bot.* 26: 90. 1988. MycoBank MB 135442.

= *Pesotum pini* (L.J. Hutchison & J. Reid) G. Okada & Seifert, *Canad. J. Bot.* 76: 1504. 1998. MycoBank MB 446360.

*Descriptions:* Hutchison & Reid (1988b: 90–91, figs 32–35, of *Hy. pini*), Kim *et al.* (2005b: 486–489, figs 1–14).

*Phylogenetic data:* Masuya *et al.* (2004), Kim *et al.* (2005a, b), Thwaites *et al.* (2005), Zipfel *et al.* (2006), Lu *et al.* (2009), Mullineux & Hausner (2009), Paciura *et al.* (2010), Six *et al.* (2011), Duong *et al.* (2012), Linnakoski *et al.* (2012), De Beer & Wingfield (2013), Taerum *et al.* (2013), Huang & Chen (2014), Wang *et al.* (2014), Romón *et al.* (2014a), Musvuugwa *et al.* (2015), Chang *et al.* (2017, 2019), Liu *et al.* (2017), De Errasti *et al.* (2018).

Notes: This species grouped in the *L. galeiforme* species complex (Fig. 5; Linnakoski *et al.* 2012, De Beer & Wingfield 2013). *Pesotum pini* has been recognised as the asexual morph of *L. radiaticola* (Kim

*et al.* 2005b). Following the One Fungus-One Name principles, the oldest name, irrespective of morph, should take precedence in the selection of the basionym. In this case, *Hyalopesotum pini* would serve that purpose. However, to avoid confusion with the name *O. pini*, currently treated as a synonym of *O. minus*, but possibly a distinct taxon (De Beer & Wingfield, 2013), we have designated *O. radiaticola* as basionym.

*Other species:* Listed in Table 1.

## **Leptographium and Grosmannia incertae sedis (Lineages III & VI)**

### **Leptographium piriforme (Lineage III)**

De Beer & Wingfield (2013) applied a relatively wide taxonomic concept for *Leptographium s.l.* and their phylogenies placed *L. piriforme* in a distinct lineage with *G. crassivaginata*. The data in the present study did not include *G. crassivaginata*. Greif *et al.* (2006) noted some morphological similarities between *L. piriforme* and *G. crassivaginata* when they described *L. piriforme*. Consequently, *G. crassivaginata* may form part of Lineage III if it were included in analyses.

*Leptographium piriforme* produces curved conidia and pear-shaped cells, distinguishing it from other *Leptographium* species (Greif *et al.* 2006, Jankowiak & Kolářik 2010). In the concatenated dataset utilised in the present study, *L. piriforme* grouped basal to Lineage I and II (Fig. 5). Although the phylogeny presented by Greif *et al.* (2006) was much smaller than that presented here, *L. piriforme* also grouped outside of the lineage containing *Leptographium* and *Grosmannia*. For the present, we have retained *L. piriforme* in *Leptographium* although its taxonomic placement clearly deserves further consideration.

### **Leptographium verrucosum (Lineage VI)**

Gebhardt *et al.* (2002) was the first to describe *L. verrucosum* (as *O. verrucosum*) and their description was based solely on morphology. De Beer & Wingfield (2013) transferred *O. verrucosum* to *Leptographium* based on LSU sequences, and their recommendation was that new species grouping with either *Leptographium* or *Grosmannia* should be described in *Leptographium*. In our LSU dataset (Fig. S1), *L. verrucosum* grouped basal to Lineage I (*Leptographium s.s.*), but this grouping was not seen in the other gene trees. For the present and until additional material is available for further analyses, we have chosen to retain it in *Leptographium*.

## **Masuyamyces (Lineage XVII)**

**Masuyamyces** Z.W. de Beer & M. Procter, **gen. nov.** MycoBank MB 840414. Fig. 12A, B.

*Etymology:* Named for Dr Hayato Masuya, a Japanese mycologist who has described 17 species of ophiostomatoid fungi, including the type species of this novel genus.

*Sexual morph:* Ascotal bases black, subglobose to globose; necks black, nearly cylindrical, curved or straight. *Ostiolar hyphae* absent or present. *Asci* evanescent, clavate to sub-globose when young. *Ascospores* hyaline, 1-celled, oblong or cylindrical in front view, allantoid in side view, globose in end view, enclosed in uniform hyaline sheath.

*Asexual morph:* *Conidiophores* macronematous, mononematous to synnematous. Hyalorhinocladia-like; *conidiophores* simple or branched, hyaline; *conidiogenous cells* annellidic, cylindrical; *conidia* hyaline, obovoid to globose, oblong to ellipsoidal, 1-celled. Pesotum-like; *conidiophores* loosely compacted, stipes hyaline to pale brown; *conidiogenous cells* hyaline annellidic; *conidia* hyaline, oblong to ellipsoidal.

*Type species:* **Masuyamyces botuliformis** (Masuya) Z.W. de Beer & M. Procter, **comb. nov.** MycoBank MB 840415.

*Basionym:* *Ophiostoma botuliforme* Masuya, Mycoscience 44: 304. 2003. MycoBank MB 489292.

*Description:* Masuya *et al.* (2003: 304, figs 11–21).

*Phylogenetic data:* Fig. 5.

*Notes on the type species:* No DNA sequence data were previously available for this species (De Beer & Wingfield 2013). Although *M. botuliformis* resembles *O. allantosporum* morphologically (Masuya *et al.* 2003), it did not group with the latter species, which groups in *Ophiostoma* (Fig. 5). Recently, sequences of *M. botuliformis* (as *O. botuliforme*) have been deposited in GenBank, which are identical to our ITS and LSU sequences. See note under *M. saponiodorus*.

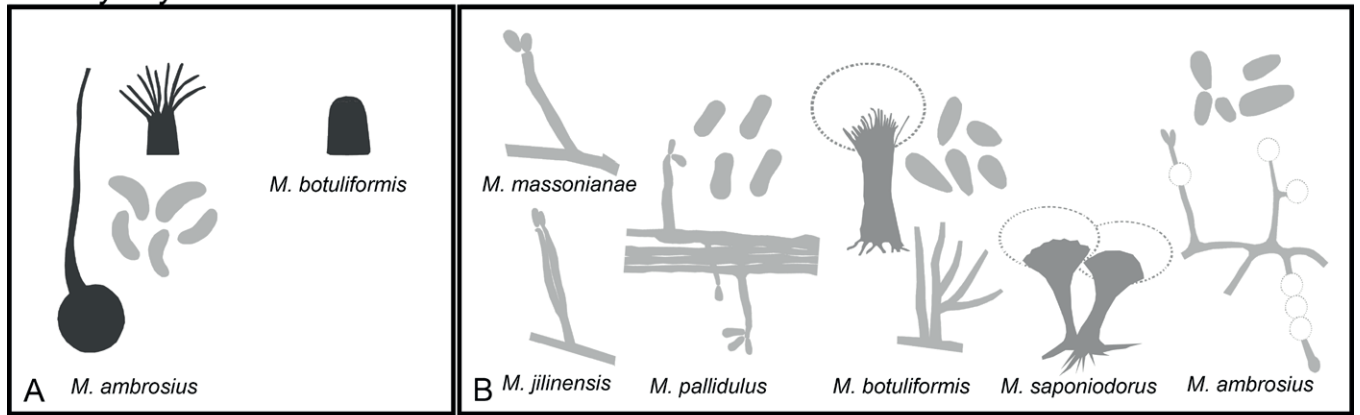
*Notes on the genus:* In our phylogenies, Lineage XVII consistently formed a monophyletic group, distinct from *Ophiostoma*. This group includes *O. ambrosium*, *O. botuliforme*, *O. pallidulum* (not included in our analyses) and *O. saponiodorum*. All described from conifers and all having reniform ascospores (Fig. 3F; Type A as categorised by De Beer & Wingfield 2013). Although *O. pallidulum* was not included in our analyses, it grouped with *O. saponiodorum* in the phylogenies of Linnakoski *et al.* (2010) and De Beer & Wingfield (2013).

The isolate of *O. ambrosium* included in our analyses is not the ex-type culture but was designated as an “isolate from type collection” by Hausner *et al.* (1993b). Our LSU sequence is almost identical to that of Hausner *et al.* (1993b), although theirs is very short. However, the morphology of this isolate does not match that of the type of *O. ambrosium*, and although this isolate is from the type collection, it may represent a different species.

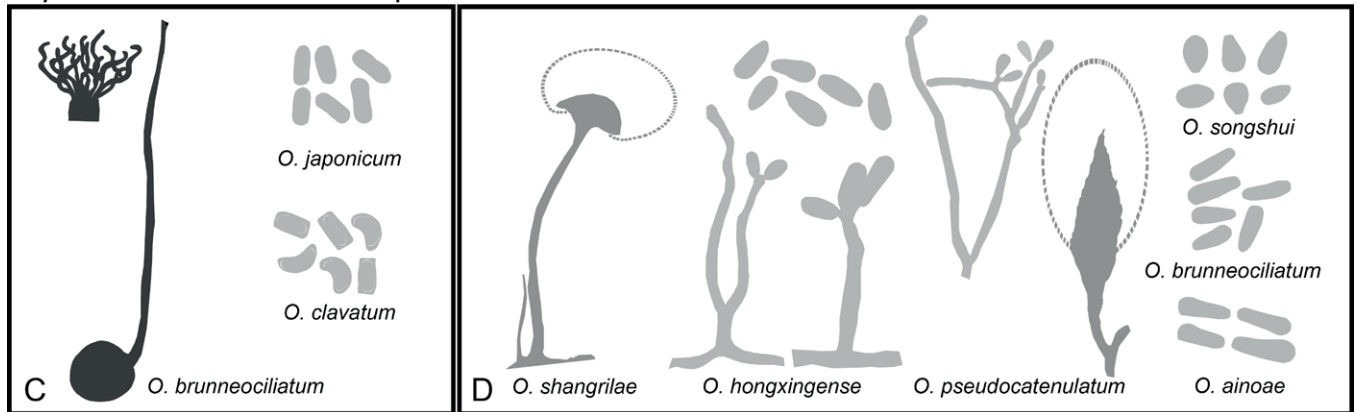
Our isolate of *O. saponiodorum* was also not the ex-type isolate for the species, but our ITS sequence is identical to the one produced by Linnakoski *et al.* (2010). The latter species grouped with isolate CMW 30883 and was used in the cross to produce the holotype of the species. Therefore, although two species in this clade are not represented by ex-type isolates, we have sufficient confidence in the sequences to justify describing this lineage as a new genus.

*Masuyamyces ambrosius* was described from *Betula albae* infested by the beetle *Trypodendron domesticum* in Great Britain (Bakshi 1950). *Masuyamyces botuliformis* was isolated from *Pinus densiflora* in Japan (Masuya *et al.* 2003), *M. pallidulus* was from *P. sylvestris* infested by *Hylastes brunneus* in Finland (Linnakoski *et al.* 2010), and *M. saponiodorus* was from *Picea abies* infested with *Ips typographus* and *Pityogenes chalcographus* in Russia as well as Finland (Linnakoski *et al.* 2010). The asexual morph of *M. botuliformis* was described as pesotum-like (Masuya *et al.* 2003), that of *M. ambrosium* as raffaelea-like (De Beer & Wingfield 2013), that of *M. pallidulus* as hyalorhinocladia-like, and that of *M. saponiodorus* as pesotum-like with a hyalorhinocladia-like synasexual morph (Linnakoski *et al.* 2010).

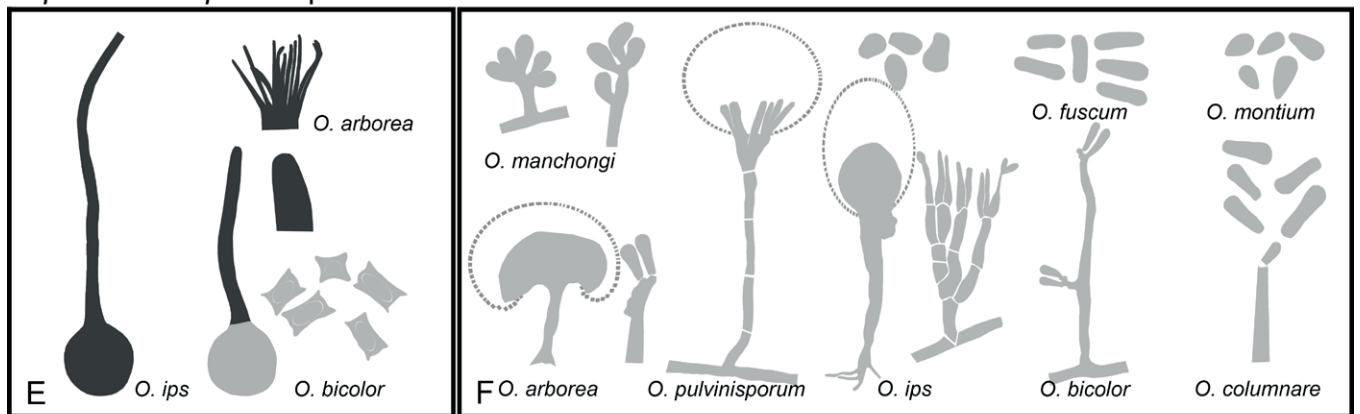
*Masuyamyces*



*Ophiostoma clavatum* complex



*Ophiostoma ips* complex



*Ophiostoma minus* complex

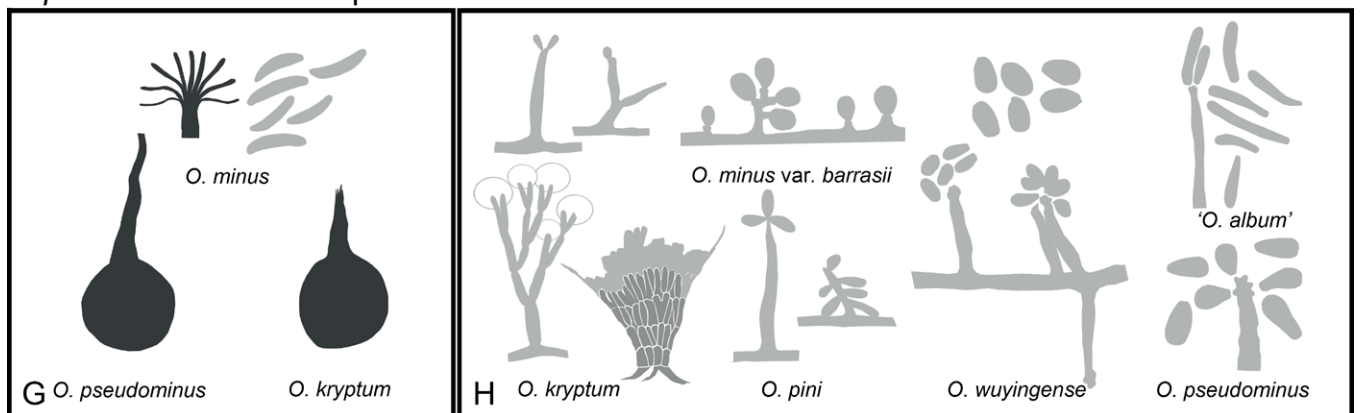


Fig. 12. Genera of the *Ophiostomatales* redrawn from published images with sexual morphs (if known) on the left and asexual morphs on the right. A, B. *Masuyamyces*. C, D. *Ophiostoma clavatum* complex. E, F. *Ophiostoma ips* complex. G, H. *Ophiostoma minus* complex. (Pale grey shading reflects hyaline to subhyaline colouration, medium-tone grey brown to dark brown and dark grey reflects fuscous black to dark black colouration).



**Other new combinations:**

**1) *Masuyamyces acarorum*** (R. Chang & Z.W. de Beer) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840416.  
*Basionym:* *Ophiostoma acarorum* R. Chang & Z.W. de Beer, MycoKeys 28: 40. 2017. MycoBank MB 823693.

*Description:* Chang *et al.* (2017: 40–41, fig. 7).

*Phylogenetic data:* Chang *et al.* (2017, 2019).

*Notes:* Sexual morph unknown. This species resides in *Masuyamyces* and grouped with *M. saponiodorus* (as *O. saponiodorum*) in the phylogenies of Chang *et al.* (2017, 2019). See note under *M. saponiodorus*.

**2) *Masuyamyces ambrosius*** (B.K. Bakshi) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840526.  
*Basionym:* *Ceratocystis ambrosia* B.K. Bakshi, Trans. Brit. Myc. Soc. 33: 116. 1950. MycoBank MB 294192.  
*Synonym:* *Ophiostoma ambrosium* (B.K. Bakshi) Georg Hausner, J. Reid & Klassen, Canad. J. Bot. 71: 1264. 1993. MycoBank MB 362662.

*Description:* Bakshi (1950: 116–118, fig. 2)

*Notes:* Sexual morph unknown. This species grouped with *M. saponiodorus* and *M. botuliformis* (Fig. 5).

**3) *Masuyamyces jilinensis*** (R. Chang *et al.*) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840417.  
*Basionym:* *Ophiostoma jilinense* R. Chang *et al.*, MycoKeys 28: 63. 2019. MycoBank MB 825086.

*Description:* Chang *et al.* (2019: 63–65, fig. 16).

*Phylogenetic data:* Chang *et al.* (2019).

*Notes:* Sexual morph unknown. This species grouped with *M. saponiodorus* (as *O. saponiodorum*) in the phylogeny of Chang *et al.* (2019), and is consequently included in the the genus. See note under *M. saponiodorus*.

**4) *Masuyamyces lotiformis*** (Z. Wang & Q. Lu) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840418.  
*Basionym:* *Ophiostoma lotiforme* Z. Wang & Q. Lu, IMA Fungus 11: 17. 2020. MycoBank MB 830612.

*Description:* Wang *et al.* (2020: 17–18, fig. 14)

*Phylogenetic data:* Wang *et al.* (2020).

*Notes:* Sexual morph unknown. This species grouped with *M. saponiodorus* (as *O. saponiodorum*) in the phylogeny of Wang *et al.* (2020), and is consequently included in the genus. See note under *M. saponiodorus*.

**5) *Masuyamyces massoniana*** M. Procter & Z.W. de Beer, **sp. nov.** MycoBank MB 840419.  
*Synonym:* *Ophiostoma massoniana* H.M. Wang & Q. Lu, MycoKeys 39: 15. 2018. *nom. inval.*, Art. 40.7. MycoBank MB 827856.

*Description:* Wang *et al.* (2018: 15–17, fig. 4).

*Holotype:* PREM 63310.

*Phylogenetic data:* Wang *et al.* (2018)

*Notes:* Sexual morph unknown. This species grouped with *M. saponiodorus* (as *O. saponiodorum*) in the phylogenies of Wang *et al.* (2018), and is thus included in the genus. See note under *M. saponiodorus*.

**6) *Masuyamyces pallidulus*** (Linnak. *et al.*) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840420.  
*Basionym:* *Ophiostoma pallidulum* Linnak. *et al.*, Persoonia 25: 86. 2010. MycoBank MB 518884.

*Description:* Linnakoski *et al.* (2010: 86, 88, fig. 9).

*Phylogenetic data:* Linnakoski *et al.* (2010, 2016), De Beer & Wingfield (2013), De Beer *et al.* (2016a, b), Chang *et al.* (2017, 2019), Wang *et al.* (2018).

*Notes:* Sexual morph unknown. Although not included in our analyses, this species was shown to consistently group with *M. saponiodorus* (as *O. saponiodorum*) and is thus treated in *Masuyamyces* (Linnakoski *et al.* 2010, 2016, De Beer & Wingfield 2013, Chang *et al.* 2017, 2019, Wang *et al.* 2018). See note under *M. saponiodorus*.

**7) *Masuyamyces saponiodorus*** (Linnak. *et al.*) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 840421.  
*Basionym:* *Ophiostoma saponiodorum* Linnak. *et al.*, Persoonia 25: 88. 2010. MycoBank MB 518885.

*Description:* Linnakoski *et al.* (2010: 88, fig. 10).

*Phylogenetic data:* Linnakoski *et al.* (2010, 2016), Six *et al.* (2011), De Beer & Wingfield (2013), Romón *et al.* (2014b), Chang *et al.* (2017, 2019), Wang *et al.* (2018).

*Notes:* *Masuyamyces saponiodorus* consistently grouped separately from what we have defined as *Ophiostoma* in our phylogenies (Fig. 5, S1–S4), and with the other species listed above in previously published phylogenies (Linnakoski *et al.* 2010, 2016, De Beer & Wingfield 2013, Chang *et al.* 2017, 2019, Wang *et al.* 2018).

***Ophiostoma* (Lineage XV)**

***Ophiostoma*** Syd. & P. Syd., Ann. Mycol. 17: 43. 1919. MycoBank MB 3614, **emend.** Z.W. de Beer & M. Procter. Figs 12C–13F.

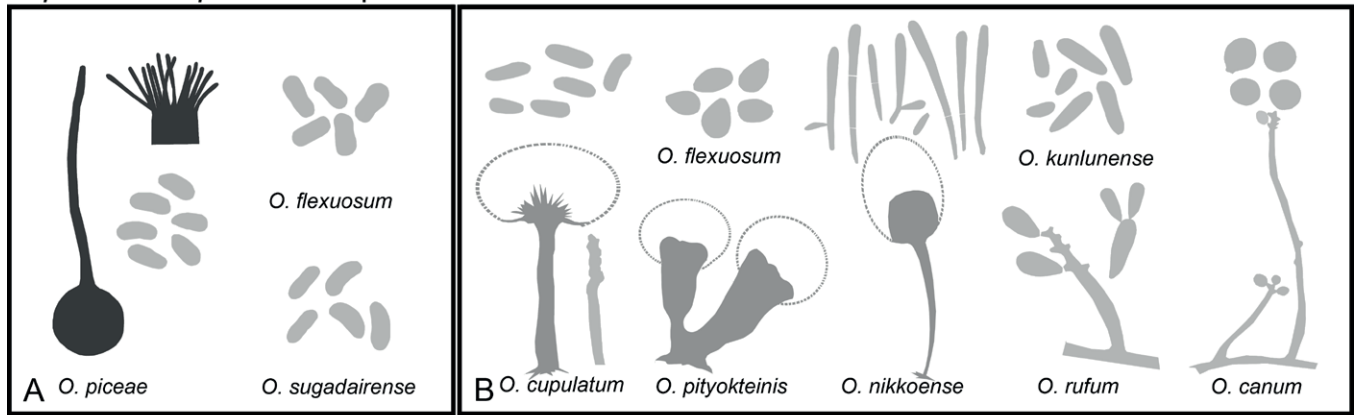
*Synonyms:* *Linostoma* Höhn., Ann. Mycol. 16: 91. 1918. MycoBank MB 2885. *nom. illegit.* Art. 53.1, De Beer *et al.* 2013a. [Type species *Linostoma piliferum* (Fr.) Höhn.].

*Pesotum* J.L. Crane & Schokn., Amer. J. Bot. 60: 347. 1973. MycoBank MB 9270. [Type species *Pesotum ulmi* (M.B. Schwarz) J.L. Crane & Schokn.].

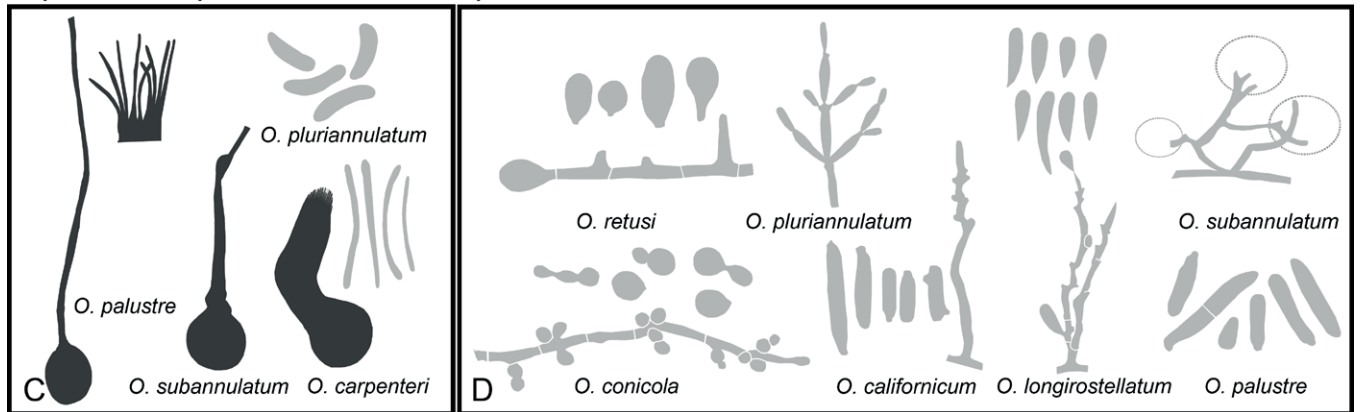
*Hyalopesotum* H.P. Upadhyay & W.B. Kendr., Mycologia 67: 801. 1975. MycoBank MB 8579. (Type species *H. introcitrinum* H.P. Upadhyay & W.B. Kendr.).

*Pachnodium* H.P. Upadhyay & W.B. Kendr., Mycologia 67: 802. 1975. Asexual synonym: MycoBank MB 9189 (Type species *P. canum* H.P. Upadhyay & W.B. Kendr.).

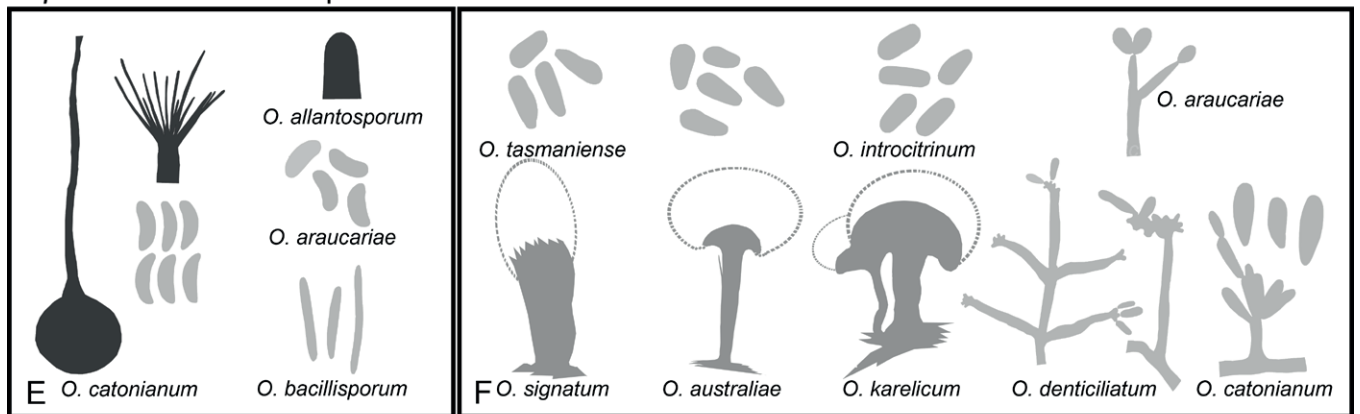
*Ophiostoma piceae* complex



*Ophiostoma pluriannulatum* complex



*Ophiostoma ulmi* complex



*Raffaelea*

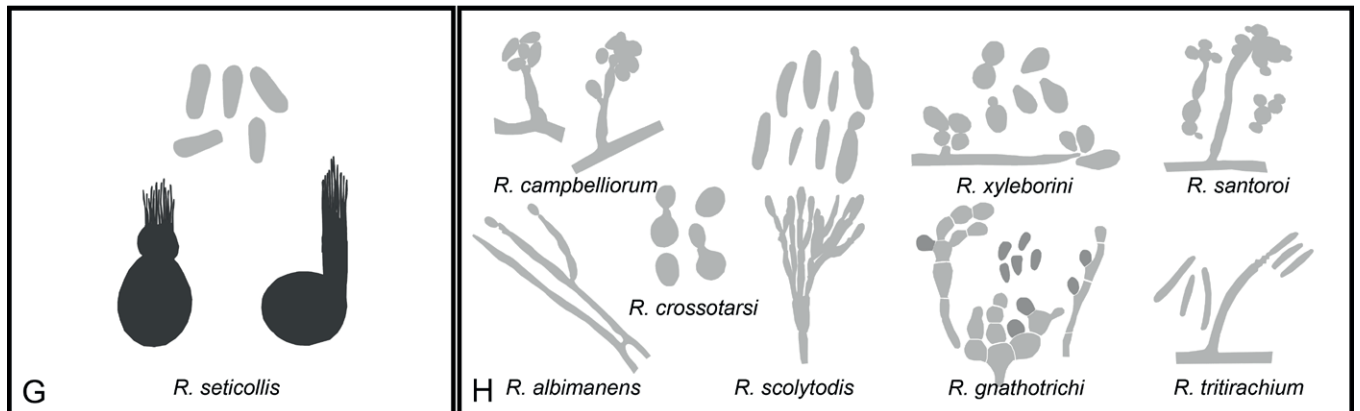


Fig. 13. Genera of the *Ophiostomatales* redrawn from published images with sexual morphs (if known) on the left and asexual morphs on the right. A, B. *Ophiostoma piceae* complex. C, D. *Ophiostoma pluriannulatum* complex. E, F. *Ophiostoma ulmi* complex. G, H. *Raffaelea*. (Pale grey shading reflects hyaline to subhyaline colouration, medium-tone grey brown to dark brown and dark grey reflects fuscous black to dark black colouration).

*Etymology:* *Ophio-* from the Greek for ‘snake-like’ and ‘*stoma*’ meaning mouth, referring to the long, tubular necks of the ascomata.

*Sexual morph:* *Ascomatal* bases black, subglobose to globose; necks black, cylindrical, straight or slightly curved. *Ostiolar hyphae* absent or present, divergent. *Asci* evanescent, clavate. *Ascospores* hyaline, 1-celled, enclosed in sheath, allantoid, reniform, cylindrical to ossiform in side view, ellipsoid in face view, globose in end view.

*Asexual morph:* *Conidiophores* macronematous, micronematous, mononematous, synnematous. Hyalorhinocladiella-like; *conidiophores* simple or branched; *conidia* hyaline, 1-celled, oblong to ellipsoid. Leptographium-like; *conidiophores* upright or prone, bases simple or rhizoid-like; *conidiogenous cells* hyaline, subcylindrical; *conidia* hyaline, 1-celled, oblong to obovoid with truncate base. Pesotum-like; *conidiophores* single or in groups, black becoming paler towards apex; stipes extending beyond conidiogenous cells, becoming seta-like structures (*O. cupulatum*); *conidia* hyaline, mostly 1-celled, oblong to ellipsoid, round apex, tapering towards base, clavate to obovoid; *conidia* elongated cylindrical or clavate with tapering towards base, 1–3-celled (*O. nikkonse*), giving rise to secondary conidia (*O. nikkoense*). Sporothrix-like; *conidiogenous cells* proliferating, sympodial, denticulate; *conidia* hyaline, 1-celled, oblong to ellipsoid, elongate or broadly cylindrical, round apex, tapering towards base, clavate or obovoid, obpyriform, giving rise to secondary spores (*O. cupulatum*, *O. flexuosum*).

*Type species:* *Ophiostoma piliferum* (Fr.) Syd. & P. Syd., Ann. Mycol. 17: 43. 1919. MycoBank MB 431882.

*Other species:* Listed in Table 1.

*Notes on the genus:* The definition of *Ophiostoma* emerging from this study relates to what was previously treated as *Ophiostoma* s.l. by De Beer & Wingfield (2013). In this case it excludes the *S. schenckii*-*O. stenoceras* complex (now *Sporothrix*) and the *O. tenellum* complex. Species in the newly defined *Ophiostoma sensu stricto* typically produce Type A or B ascospores (Fig. 3F, G; as categorised by De Beer & Wingfield 2013) and a variety of asexual morphs including those that are sporothrix-like, pesotum-like, hyalorhinocladiella-like; some having more than one morph and commonly a continuum between these morphs (De Beer & Wingfield 2013).

### Species complexes:

#### The *O. clavatum* complex

The *O. clavatum* complex was defined by Linnakoski *et al.* (2016). Species in this complex generally have rectangular to cylindrical shaped ascospores (Fig. 3F; Type A as categorised by De Beer & Wingfield 2013), spirally coiled ostiolar hyphae that are brown in colour and they produce pesotum-like asexual morphs (Mathiesen-Käärik 1960, Linnakoski *et al.* 2016). These fungi are found in Eurasia and are mostly associated with conifer-infesting bark beetles residing in the genus *Ips* and some species cause blue stain in the sapwood of trees (Linnakoski *et al.* 2016).

*Ophiostoma ainoae* and *O. tapionis* grouped peripherally to other species in the *O. clavatum* complex in the datasets of Linnakoski *et al.* (2016). *Ophiostoma ainoae* has ascospores similar in shape to species in the *O. ips* complex, but groups within the *O. clavatum* complex (Linnakoski *et al.* 2016). *Ophiostoma ainoae*

also has a hyphal morphology similar to that of *O. clavatum* but it grouped peripheral to that complex (Linnakoski *et al.* 2016). Due to its morphological similarity with other species in the complex, *O. ainoae* is best treated as part of the *O. clavatum* species complex. This grouping was also supported in our analyses (Fig. 5).

#### The *O. ips* complex

The *O. ips* complex was first defined by De Beer & Wingfield (2013). Species in the complex all have cylindrical ascospores in a pillow-shaped sheath (Fig. 3H; Type E as categorised by De Beer & Wingfield 2013) and this distinguishes them from other species in *Ophiostoma*. These species form pesotum- to hyalorhinocladiella-like asexual morphs (De Beer & Wingfield 2013). Members of this complex are associated with bark beetles in the genera *Ips* and *Dendroctonus*, infesting conifers mostly in North America and areas where pine trees have been introduced (Upadhyay 1981, Zhou *et al.* 2004a, Linnakoski *et al.* 2010).

The ex-type isolate of the asexual species *Hyalorhinocladiella ips* (CMW 14175) grouped in our analyses within the *O. ips* complex, similar to the results of De Beer & Wingfield (2013). *Hyalorhinocladiella ips* was originally described as *Tuberculariella ips* (Leach *et al.* 1934), later treated in *Ambrosiella* (Batra 1967) and most recently in *Hyalorhinocladiella* (Harrington *et al.* 2010). This fungus has been suggested to represent the asexual morph of *O. montium*, because the two species share morphological similarities and there are minimal differences in their sequence data (Massoumi Alamouti *et al.* 2009, De Beer & Wingfield 2013, De Beer *et al.* 2013b). In our analyses (Fig. 5) *O. montium* and “*H. ips*” grouped very close to each other. De Beer *et al.* (2013b) formally listed *H. ips* as synonym of *O. montium* (Rumbold 1941), even though *H. ips* is the older of the two names (Leach *et al.* 1934) and should thus be designated as basionym for the species. However, the epithet “*ips*” is already in use for *O. ips*, the name bearing species of this complex, that has *Ceratostomella ips* (Rumbold 1931) as basionym. To avoid the creation of a later homonym by using *H. ips* as basionym, we have chosen to select *Ceratostomella montium* (Rumbold 1941) as basionym for the species and for which *O. montium* (Von Arx 1952) is then the appropriate current name. The *O. ips* complex formed a well-supported lineage that might be excluded from *Ophiostoma* s.s. in future to be treated as a distinct genus. However, for the present and in the absence of more robust datasets, we have retained species in this complex in *Ophiostoma* s.s.

#### The *O. minus* complex

The *O. minus* complex was well supported in our phylogenies even though this was not true in the phylogenies of De Beer & Wingfield (2013). The *O. minus* complex was first defined by Jacobs & Kirisits (2003). Species in this complex produce hyalorhinocladiella-like asexual morphs (Fig. 3A; as categorised by De Beer & Wingfield 2013) and have been isolated from conifers in North America and Europe. *Ophiostoma minus* is a well-known causal agent of blue stain in conifers. It is associated with the southern pine beetle (*Dendroctonus frontalis*), a native but invasive pest in the USA (Jacobs & Kirisits 2003, Gorton *et al.* 2004).

It must be noted that our phylogenies included isolates of only the North American form of *O. minus* and *O. pseudominus*, both available in the CMW collection. This was due to the fact that there were no available cultures of other species included in the complex by previous authors (Jacobs & Kirisits 2003, Gorton *et al.* 2004, Linnakoski *et al.* 2010, De Beer & Wingfield 2013).

### The *O. piceae* complex

Harrington *et al.* (2001) first defined the *O. piceae* complex, but the complex was not applied by De Beer & Wingfield (2013). Because the complex did not have any phylogenetic support in their trees, De Beer and Wingfield (2013) treated the species in the complex as part of *Ophiostoma* s.s. Yin *et al.* (2016) redefined the *O. piceae* complex, including the description of three new species described from spruce-infesting bark beetles in China. The two sub-clades seen to be formed by the *O. piceae* complex (Harrington *et al.* 2001) are now known as the *O. ulmi* complex and the *O. piceae* complex. The *O. ulmi* complex includes what was previously referred to as the 'hardwood clade', and the newly redefined *O. piceae* complex includes what was previously referred to as the 'conifer clade' (Harrington *et al.* 2001, Grobbelaar *et al.* 2010, 2011, Kamgan Nkuekam *et al.* 2011, De Beer & Wingfield 2013, Yin *et al.* 2016). Species in this complex form ascomata with long necks of up to 500 µm and can form either sporothrix- or pesotum-like asexual morphs, or both, while some form hyalorhinocladial-like asexual morphs (Fig. 3A, C, E; as categorised by De Beer & Wingfield 2013). Members of this complex have been isolated from conifers mostly in the Northern Hemisphere, and one species (*O. cupulatum*) was described from New Zealand (Yin *et al.* 2016). In our phylogenies, the *O. piceae* complex grouped distinct from the *O. ulmi* complex.

### The *O. pluriannulatum* complex

The *O. pluriannulatum* complex was initially defined as the *O. multiannulatum* complex (Villarreal *et al.* 2005) and later renamed to the *O. pluriannulatum* complex (Kamgan Nkuekam *et al.* 2008, Zanzot *et al.* 2010, De Beer & Wingfield 2013). Ascospores of species in the complex are allantoid (Fig. 3F; Type A in De Beer & Wingfield 2013) (Hunt 1956, Kamgan Nkuekam *et al.* 2008, Zanzot *et al.* 2010, De Beer & Wingfield 2013). This is with the exception of *O. carpenteri* that has Type B (Fig. 3G) narrowly clavate ascospores (Hausner *et al.* 2003, De Beer & Wingfield 2013). Other than *O. carpenteri*, all members of the *O. pluriannulatum* complex have very long ascomatal necks relative to other *Ophiostoma* species (Zanzot *et al.* 2010, De Beer & Wingfield, 2013). *Ophiostoma carpenteri* has very short necks but does produce a sporothrix-like asexual morph as in all other members of the complex (Hausner *et al.* 2003, De Beer & Wingfield 2013). Species in this complex have been found in Eurasia, North America and Africa on conifers and hardwoods, and some associated with bark beetles in the genera *Ips* and *Dendroctonus* (Zhou *et al.* 2004a, Linnakoski *et al.* 2010, Pacuira *et al.* 2010). This complex may represent a discrete genus, but our analyses were not sufficiently robust to support such a distinction.

### The *O. ulmi* complex

The *O. ulmi* complex was first known as the 'hardwood clade' in the *O. piceae* complex (Harrington *et al.* 2001, Linnakoski *et al.* 2010). It was later referred to as the *O. quercus* complex (Kamgan Nkuekam *et al.* 2011), until De Beer & Wingfield (2013) defined it as the *O. ulmi* species complex. Most of the members of the complex produce allantoid ascospores (Fig. 3F; Type A) that lack sheaths (Hunt 1956, Brasier 1991, De Beer & Wingfield, 2013). Species in this complex occur in Eurasia, Australia, Africa and North and South America and are associated with a variety of bark beetles (Upadhyay 1981, Brasier 1991, Brasier & Mehrotra 1995, Villarreal *et al.* 2005, Harrington *et al.* 2001, Kamgan Nkuekam *et al.* 2010, 2011, Linnakoski *et al.* 2008, 2009, Grobbelaar *et al.* 2010, Pacuira *et al.* 2010). De Beer & Wingfield (2013) chose to have *O. ulmi* as the name bearing species for this complex, justified because

it is the best-known species in this complex, as one of the causal agents of Dutch Elm Disease (DED). *Ophiostoma novo-ulmi* and *O. himal-ulmi* are also causal agents of DED (Brasier 1991, Harrington *et al.* 2001). DED is one of the most catastrophic tree disease pandemics in the Northern Hemisphere, leading to the death of large populations of Elm trees (Brasier 1979, 1991, Gibbs 1978). Another species in this complex, *O. quercus*, is associated with substantial economic losses due to sapstain in *Quercus* spp. (Harrington *et al.* 2001).

*Ophiostoma bacillisporum*, *O. torulosum* and *O. undulatum* have asexual morphs that are different in morphology to other members of the *O. ulmi* complex. Their asexual morphs are mycelial while other members of the complex form sporothrix- and pesotum-like asexual morphs. The ascospores of the species are, however, similar to those in the *O. ulmi* complex (De Beer & Wingfield, 2013). We have supported the decision of De Beer & Wingfield (2013) to include species residing in what was known as the *O. quercus* complex (Kamgan Nkuekam *et al.* 2011) in the *O. ulmi* complex. This decision is justified based on the fact that *O. quercus* groups within the *O. ulmi* complex. However, our analyses grouped *O. torulosum* outside the *O. piceae* complex (Fig. 5) and its position requires further consideration.

### Group H

De Beer & Wingfield (2013) included *O. triangulosporium* in the *O. ulmi* complex but noted that its unique ascospore morphology (allantoid ascospores with triangular sheaths) suggested that its placement in the complex required further study, including inspection of the type material and a greater number of isolates. In our analyses (Fig. 5), *O. triangulosporium* grouped peripheral to other species in the *O. ulmi* complex.

### Group I

*Ophiostoma macrosporum* and an undescribed *Ophiostoma* species (previously treated as a *Hyalorhinocladialla* sp.) formed a small lineage outside of any of the species complexes in *Ophiostoma*.

### Group J

The type species of *Ophiostoma*, *O. piliferum*, grouped on its own within *Ophiostoma*. Although it is the type of the genus, it does not group in any species complex (De Beer & Wingfield 2013, Yin *et al.* 2016, De Beer *et al.* 2016a, b).

### Group K

*Ophiostoma tetropii* grouped peripheral to the *O. minus* and *O. piceae* complexes (Fig. 5). Linnakoski *et al.* (2010) included *O. tetropii* in the *O. minus* complex. However, the ascospores of *O. tetropii* have a distinct morphology different to species in the *O. minus* complex (De Beer & Wingfield 2013). The phylogenies of De Beer & Wingfield (2013) also showed that *O. tetropii* grouping separately from the *O. minus* complex and it clearly requires further study.

### *Ophiostoma incertae sedis* (Lineages XVIII, XX & XXIII)

#### *Ophiostoma valdivianum* (Lineage XVIII)

As mentioned above, *O. valdivianum* formed a lineage with *S. fumea* in the phylogenies of De Beer *et al.* (2016a), grouping basal to most of *Sporothrix*. However, in the phylogenies arising from the present study, these two species did not group together.

***Ophiostoma angusticollis* and *O. denticulatum* (Lineage XX)**

*Ophiostoma angusticollis* and *O. denticulatum* consistently formed a lineage distinct from *Ophiostoma*. In the phylogenies of De Beer & Wingfield (2013), *O. angusticollis* formed a lineage with *O. sejunctum* (not included in the present study) close to the *O. tenellum* complex (Lineage XIII) but distinct from *Ophiostoma*. We have chosen not to describe this lineage as a new genus because we were not able to include the holotype of *O. angusticollis*.

***Ophiostoma noisomeae* (Lineage XXIII)**

*Ophiostoma noisomeae* consistently grouped distinct from *Ophiostoma* in our datasets. In the phylogenies of De Beer *et al.* (2016a), *O. noisomeae* also grouped distinct from *Ophiostoma*.

***Paleoambrosia* (No sequence data available)**

***Paleoambrosia*** Poinar & F.E. Vega, Fungal Biol. 122: 1160. 2018. MycoBank MB 840457. *nom. inval.*, Art. F.5.1.

**Etymology:** ‘From the Greek “palaios” = ancient, and the Greek “ambrosia” = immortal, referring to the fossilized ambrosial fungus discovered with a Platypodine beetle in ~100 million-year-old amber in Myanmar’ (Poinar & Vega 2018).

**Sexual morph:** Unknown.

**Asexual morph:** *Conidiophores* borne in sporodochia, simple, black. *Conidia* black, 1-celled, globose to obovoid, borne in slimy droplet terminally. Yeast-like cells present in mycangium.

**Type species:** *Paleoambrosia entomophila* Poinar & F.E. Vega, Fungal Biol. 122(12): 1160 (2018). MycoBank MB 840458. *nom. inval.*, Art. F.5.1.

*No other species known at present.*

**Notes:** This genus was recently described from a specimen found in amber and was included in the current study for completeness, despite the fact that its placement in the *Ophiostomatales* (Poinar & Vega 2018) is open to debate. The fossil beetle associated with this fungus could have been misidentified and might not be a member of the Platypodinae. Likewise, whether the cavity shown on the beetle reflects a functional mycangium is unclear. The growth form of the fungus growing alongside the beetle is unusual for any beetle-related ophiostomatalean fungus, and mucilage-bound phialidic spores could be those of an asexual morph of an entomopathogenic or another fungus producing phialidic conidiophores.

***Raffaelea* (Lineage XII)**

***Raffaelea*** Arx & Hennebert, Mycopathol. Mycol. Appl. 25: 310. 1965. MycoBank MB 9685, **emend.** Z.W. de Beer & M. Procter. Fig 13G, H.

**Etymology:** Named for the Italian mycologist and plant pathologist, Prof. Raffaele Ciferri (1897–1964).

**Sexual morph:** *Ascomatal* bases black, subglobose to globose; necks black, straight or curved. *Ostiolar hyphae* present or absent. *Asci* evanescent. *Ascospores* hyaline, 1-celled or rarely 2-celled, cylindrical to oblong, enclosed in hyaline rectangular sheath.

**Asexual morph:** *Colony* confluent, mucilaginous. *Conidiophores* micronematous, macronematous, mononematous, solitary or aggregated in sporodochia, hyaline, simple or branched, moniloid. *Conidiogenous cells* flask-shaped, proliferating percurrently or sympodially, with denticles, inconspicuous scars or annellations. *Conidia* hyaline, ellipsoidal, obovoid, globose, pyriform, sometimes T- or Y-shaped, 1-celled, producing secondary cells through budding. Associated with ambrosia beetles.

**Type species:** *R. ambrosiae* Arx & Hennebert, Mycopathol. Mycol. Appl. 25: 310. 1965. MycoBank MB 338171.

**Other species:** Listed in Table 1.

**Notes:** *Raffaelea* was originally described to accommodate a number of fungal mutualists of wood-boring ambrosia beetles (Von Arx & Hennebert 1965). In the same paper, Von Arx & Hennebert (1965) validated a similar genus, *Ambrosiella*, with a mode of conidial development different to that in *Raffaelea*. However, confusion persisted regarding the generic placement of species in these two genera until DNA sequence data showed that *Ambrosiella* belonged in the *Ceratocystidaceae* (*Microascales*) and *Raffaelea* in the *Ophiostomatales* (Batra 1967, Cassar & Blackwell 1996, Massoumi Alamouti *et al.* 2009, Harrington *et al.* 2010, De Beer *et al.* 2013a, 2014). Species of *Raffaelea* have reduced conidiophore morphology, distinguishing them from other Ophiostomatalean genera (De Beer & Wingfield 2013). All species in the genus are mutualists of ambrosia beetles in the sub-families *Scolytinae* and *Platypodinae* (*Curculionidae*), respectively, in North America, South Africa, Europe and Asia (Harrington *et al.* 2010, Hulcr & Stelinski 2017).

Prior to the study of Musvuugwa *et al.* (2015), *Raffaelea* was considered as an exclusively asexual genus. Musvuugwa *et al.* (2015) described a *Raffaelea* species forming sexual structures and emended the generic description of *Raffaelea* to accommodate these structures. In our analyses, *R. vaginata* (labelled as Lineage X) did not consistently group within *Raffaelea* (see below). However, our analyses support the inclusion of *R. seticollis* in *Raffaelea*, which was one of the other two sexually reproducing species treated in *Raffaelea* by Musvuugwa *et al.* (2015). This species was originally described from ambrosial galleries in a hemlock (*Tsuga canadensis*) stump in New York State (Davidson 1966) but has not been recorded again. Musvuugwa *et al.* (2015) also transferred *O. deltoideosporum* to *Raffaelea* based on a short LSU sequence of the fungus produced by Hausner *et al.* (1993b), and morphological similarities to *O. seticolle*. We did not have access to material of this species and could therefore not include it in our analyses. For the present, we have followed the suggestion of Musvuugwa *et al.* (2015) and include it in *Raffaelea*.

***Raffaelea incertae sedis* (Lineage X)*****Raffaelea vaginata***

**Notes:** This species was described from a beetle in the genus *Lanurgus* collected from a native tree in the Southern Cape of South Africa (Musvuugwa *et al.* 2015). The fungus formed a sexual morph similar to *O. deltoideosporum* and *O. seticolle* that grouped in *Raffaelea* in the study of De Beer & Wingfield (2013). As stated above, analyses of our data supported the inclusion of *R. seticollis* (*O. seticolle*) in *Raffaelea*. Because *R. vaginata* did not consistently group within *Raffaelea* in our analyses, it is not included in our narrower definition of *Raffaelea*. While it might represent a novel

genus, there is insufficient information to make this decision and it is thus treated as *incertae sedis*.

## **Sporothrix (Lineage XIV)**

**Sporothrix** Hektoen & C.F. Perkins, J. Exp. Med. 5: 80. 1900. MycoBank MB 10046, **emend.** Z.W. de Beer *et al.*, Stud. Mycol. 83: 171. 2016. Figs 14, 15.

*Synonyms:* *Spumatoria* Masee & E.S. Salmon, Ann. Bot. (Oxford) 15: 350. 1901. MycoBank MB 5175. [Type species *Spumatoria longicollis* Masee & E.S. Salmon, Ann. Bot. (Oxford) 15: 351 (1901)]. *Sporotrichopsis* Guég., Arch. Parasitol. 15: 104. 1911. MycoBank MB 10048. [Type species *S. beurmannii* (Matr. & Ramond) Guég.; *nom. inval.*, Art. 38.1].

*Dolichoascus* Thibaut & Ansel, Compt. Rend. Hebd. Seances Acad. Sci. 270: 2173. 1970. MycoBank MB 1684. (Type species *D. schenckii* Thibaut & Ansel; *nom. inval.*, Art. 40.1).

*Etymology:* The name is derived from the Latin for 'spore hair' (De Hoog 1974).

*Sexual morph:* *Ascomatal* bases black, globose; necks black, becoming paler towards apex, straight or slightly curved. *Ostiolar hyphae* parallel to divergent. *Asci* evanescent. *Ascospores* hyaline, 1-celled, allantoid to reniform in side view, almost triangular-shaped, ovoid to oblong.

*Asexual morph:* *Conidiophores* micronematous, semi-macronematous, mononematous, simple. *Conidiogenous cells* showing sympodial growth, terminal or intercalary, cylindrical, denticulate or not denticulate, hyaline. *Conidia* hyaline to subhyaline, 1-celled, subglobose to oblong, obovoid, clavate to strongly curved, guttuliform to fusiform with round apices and pointed base that sometimes slightly curved, sometimes slightly curved at base; (pathogenic clade and *S. inflata* complex) borne directly on hyphae (sessile) brown to dark brown, subglobose to globose, narrowly obovoid, ellipsoid, 1-celled. *Secondary conidia* borne by yeast-like budding, absent or present.

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

*Other species:* Listed in Table 1.

*Notes:* *Sporothrix* was described as part of a medical case study concerning a child who had contracted a fungal infection after injuring his finger with a hammer (Hektoen & Perkins 1900). The fungus isolated from the infection was described as *Sporothrix schenckii*. The epithet referred to B.R. Schenck who described, but did not name a similar fungus in an earlier study. The genus description of *Sporothrix* by Hektoen & Perkins (1900) was invalid, and the name was validated years later by Nicot & Mariat (1973). In the late 1960's, *S. schenckii* was suggested to represent the asexual morph of *O. stenoceras* (Nicot & Mariat 1973), and subsequently the asexual morphs of many other *Ophiostoma* species were also treated in *Sporothrix* under the dual nomenclature system (De Hoog 1974, De Beer & Wingfield 2013).

The phylogenetic placement of *S. schenckii* in the *Ophiostomatales* based on ribosomal DNA sequences by Berbee & Taylor (1992) became the first example where asexual (anamorph) and sexual (teleomorph) genera were connected based on phylogenetic inference. This represented a first important step

towards the abandonment of the the dual nomenclature system for the fungi, which culminated in the Amsterdam Declaration (Hawksworth *et al.* 2011) and subsequent changes to the Code where one fungus could only have one species name.

Following the adoption of the One Fungus-One Name convention, De Beer & Wingfield (2013) listed *Sporothrix* as a synonym of *Ophiostoma*, with the type species of *Sporothrix* (*S. schenckii*) forming part of the *S. schenckii*-*O. stenoceras* complex in a broad concept for *Ophiostoma*. De Beer & Wingfield (2013) noted that this species complex could represent a genus separate from other species in *Ophiostoma* s.l. However, the available data at the time were insufficient to formally separate the two genera. In a more comprehensive study including sequences of all *Sporothrix* spp. and all *Ophiostoma* spp. with *Sporothrix* asexual morphs, De Beer *et al.* (2016a) showed that the *S. schenckii*-*O. stenoceras* complex formed a well-supported monophyletic lineage, distinct from other species in *Ophiostoma*. Because this lineage accommodated the type species of *Sporothrix*, they reinstated the genus, transferring all *Ophiostoma* species in this lineage to *Sporothrix*. De Beer *et al.* (2016a) also emended the description of *Sporothrix* to include sexual morphs. Furthermore, they defined several species complexes within *Sporothrix*. The analyses emerging from the present study support the separation of *Sporothrix* and *Ophiostoma* based on strong monophyletic lineages. There are a few exceptions where species formed independent lineages and these are discussed below.

### **Species complexes:**

See De Beer *et al.* (2016a) and below.

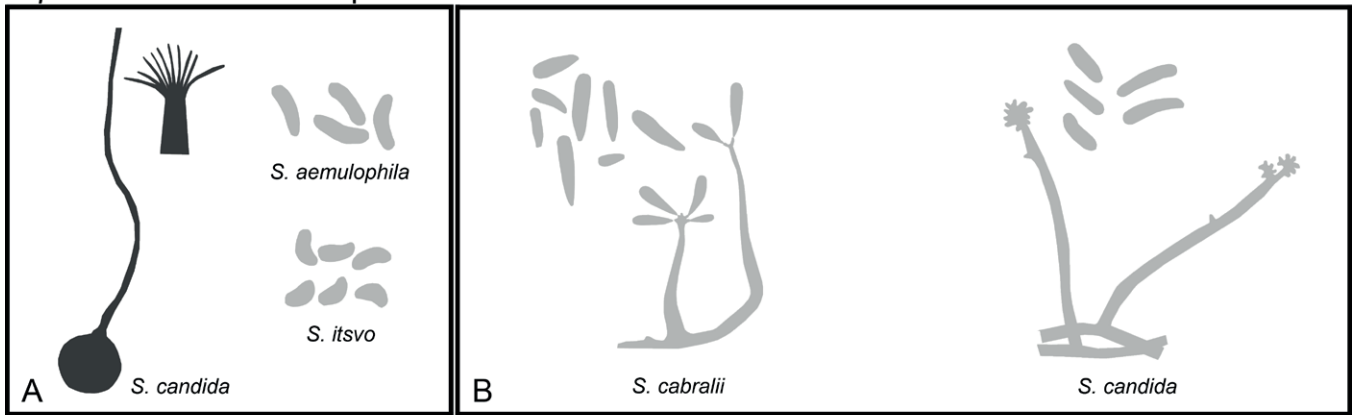
#### **The *S. candida* complex**

The *S. candida* complex accommodates four species that have been described from hardwoods in South Africa (Kamgan Nkuekam *et al.* 2012, Musvuugwa *et al.* 2016) and one species from hardwoods in Argentina (De Errasti *et al.* 2016). *Sporothrix itsvo* was previously included in this species complex, but it grouped within the *S. gossypina*/*S. stenoceras* complex in our phylogenetic analyses (Fig. 5).

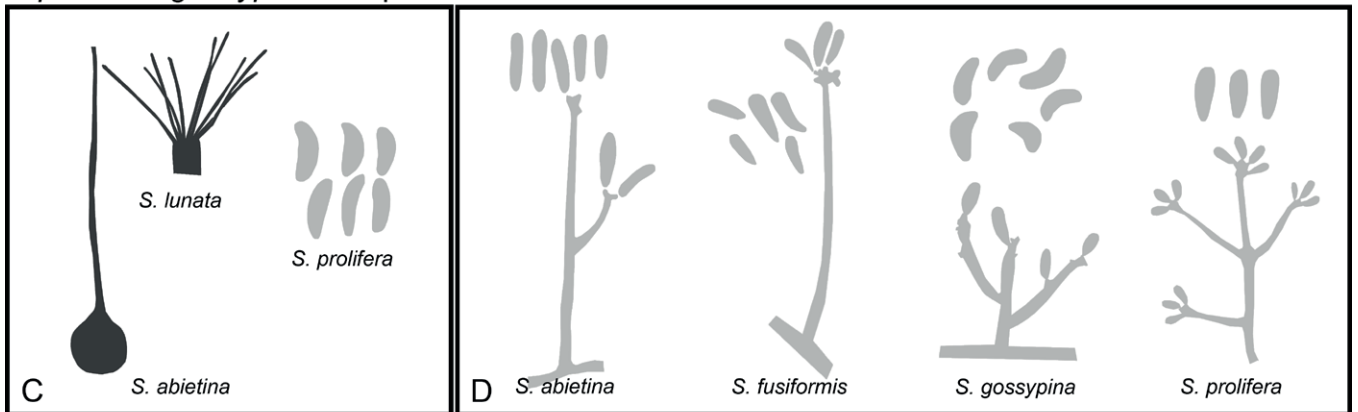
#### **The *S. inflata* complex**

The *S. inflata* complex accommodates species that have been isolated from oak in Europe, soil in Europe, Canada and Malaysia (De Beer *et al.* 2016a). It also includes the epitype isolate of *Spumatoria longicollis*, a coprophilous fungus. In a recent study forming part of The Genera of Fungi project (<http://www.mycobank.org>), Giraldo *et al.* (2017) showed an isolate of the monotypic genus *Spumatoria* (*Sp. longicollis*) grouping within *Sporothrix*, based on ITS, LSU and *BT* sequence data. These authors considered this as the first report of the fungus after it was initially described. The type of this species has been lost (De Beer *et al.* 2014) and consequently Giraldo *et al.* (2017) designated an epitype, isolated from cow dung in the Netherlands, which was used in the present study. Although this species has a sporothrix-like asexual morph, its septate ascospores distinguished it from all other ophiostomatalean species. Furthermore, its coprophilous nature and pale coloured ascomata distinguish it from other *Sporothrix* species (De Beer *et al.* 2014, Giraldo *et al.* 2017). De Beer *et al.* (2013a) excluded *Spumatoria* from the *Ophiostomatales*, based on these atypical characteristics and characteristics shared with *Kathistes*, which is phylogenetically distant from the *Ophiostomatales*. Our analyses included LSU and *TEF-1 $\alpha$*  sequence data for the epitype isolate,

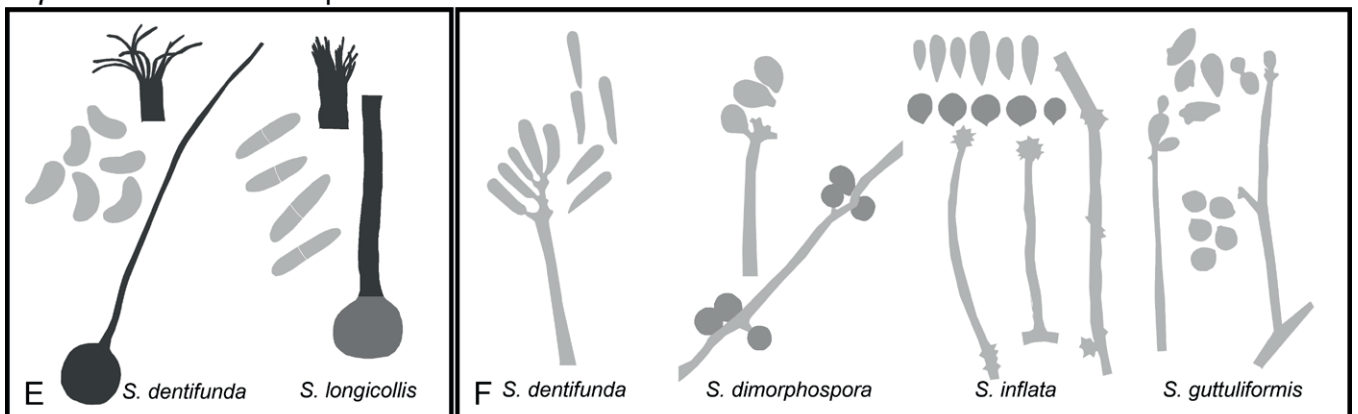
*Sporothrix candida* complex



*Sporothrix gossypina* complex



*Sporothrix inflata* complex



*Sporothrix pallida* complex

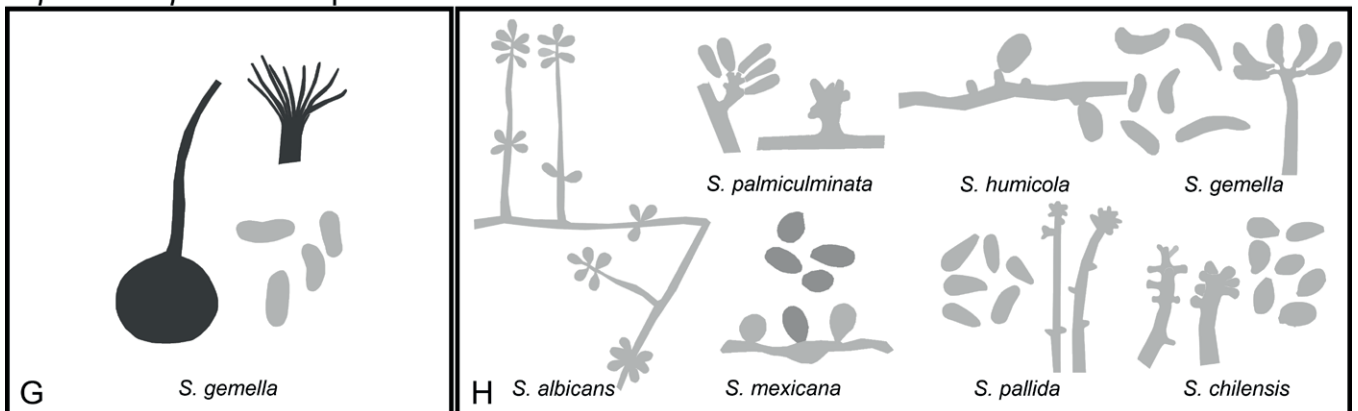
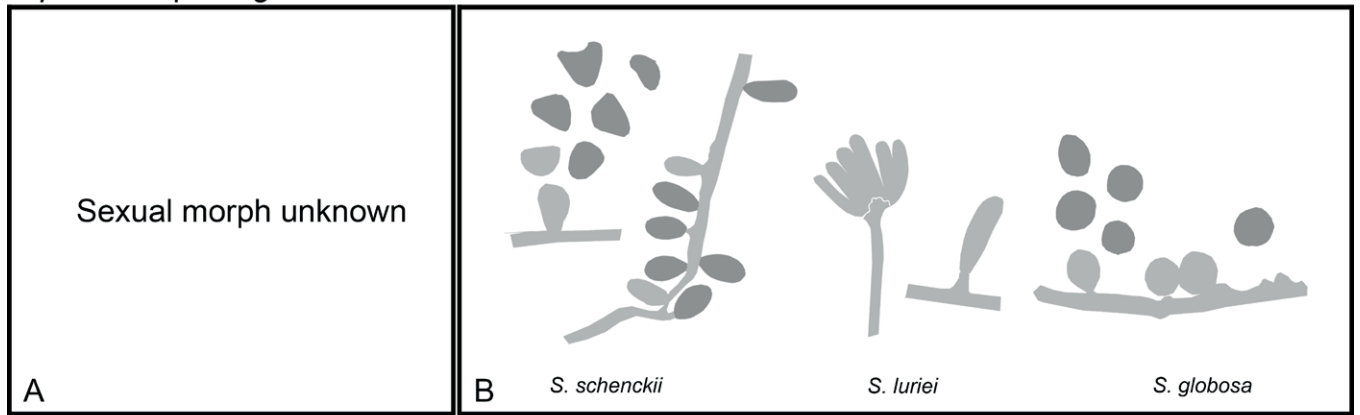
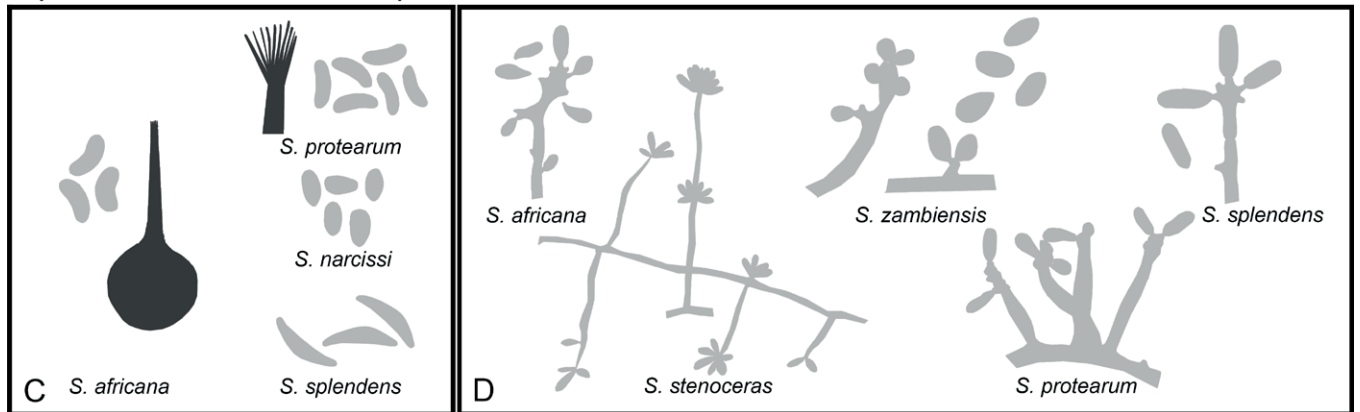


Fig. 14. Genera of the *Ophiostomatales* redrawn from published images with sexual morphs (if known) on the left and asexual morphs on the right. A, B. *Sporothrix candida* complex. C, D. *Sporothrix gossypina* complex. E, F. *Sporothrix inflata* complex. G, H. *Sporothrix pallida* complex. (Pale grey shading reflects hyaline to subhyaline colouration, medium-tone grey brown to dark brown and dark grey reflects fuscous black to dark black colouration).

*Sporothrix* pathogenic clade



*Sporothrix stenoceras* complex



**Fig. 15.** Genera of the *Ophiostomatales* redrawn published images with sexual morphs (if known) on the left and asexual morphs on the right. **A, B.** *Sporothrix* pathogenic clade. **C, D.** *Sporothrix stenoceras* complex. (Pale grey shading reflects hyaline to subhyaline colouration, medium-tone grey brown to dark brown and dark grey reflects fuscous black to dark black colouration).

which placed it within the *S. inflata* species complex (Figs 5, S1, S3).

**The *S. stenoceras* and *S. gossypina* complexes**

The *S. stenoceras* and *S. gossypina* species complexes formed an aggregated lineage in the analyses of our datasets (Figs 5, S1, S3). Interestingly, the lineage within the *S. stenoceras* complex including species isolated from *Protea* (De Beer et al. 2016a, Ngubane et al. 2018), and *S. gemella* (also from *Protea*), formed a lineage distinct from the other species in these complexes, none of which are associated with *Protea*.

The *S. gossypina* complex accommodates species that have diverse ecologies (De Beer et al. 2016a). Some species are associated with conifer-infesting bark beetles (Davidson 1971, Marmolejo & Butin 1990, Zhou et al. 2004a, 2006, Lu et al. 2009, Linnakoski et al. 2010, Six et al. 2011, Taerum et al. 2013), others specifically with pine-infesting bark beetles (Davidson 1971, Zhou et al. 2006, Rom3n et al. 2014a, b), and a few species that have been isolated from stained oak wood (Aghayeva et al. 2004). Interestingly, there is also a species isolated from cankers on chestnut caused by the aggressive tree pathogen *Cryphonectria parasitica* (Davidson 1978). Species are widely distributed in the USA, Europe, Asia and South Africa (De Beer et al. 2016a).

*Sporothrix stenoceras* has been isolated from soils and hardwoods on many continents. This could explain why it grouped with species in the *S. gossypina* complex.

*Sporothrix gemella* was previously included in the *S. pallida* complex, but it grouped within the complex in the analyses of our

combined dataset (Fig. 5). This species is found on *Protea* species in South Africa and is vectored by mites, a niche similar to that of *S. splendens* (Roets et al. 2013, De Beer et al. 2016a).

*Ophiostoma ponderosae* grouped in this species complex in the analyses of our combined dataset (Fig. 5). The LSU sequence generated by De Beer et al. (2016a) for the same isolate placed this species in *Ophiostoma* s.s. Our sequence data for *O. ponderosae* differed from the sequence generated by De Beer et al. (2016a) in only a small number of bases.

**The *S. pallida* complex**

Three species forming part of the *S. pallida* complex (*S. pallida*, *S. mexicana* and *S. chilensis*) have been reported as rare and opportunistic pathogens of humans, but mostly occurring in soil along with other species in this complex. Two species are associated with *Protea* species occurring in South Africa. Species in this complex have been found in Japan, Mexico, Chile, England and South Africa (De Beer et al. 2016a).

**The pathogenic clade**

Most *Sporothrix* species are relatively harmless to humans, but there are four species (*S. schenckii*, *S. luriei*, *S. brasiliensis* and *S. globosa*) that are human and animal pathogens. These species are the causal agents of the disease known as sporotrichosis (Teixeira et al. 2014). All four species form pigmented blastoconidia, in addition to the more typical sporothrix-like morphology of the asexual morphs. This is possibly an adaptation to both the soil inhabiting and animal-pathogenic lifestyle of these fungi (De



Beer *et al.* 2016a). Collectively, these pathogens have an almost global distribution. *Sporothrix schenckii* has been isolated in the Americas, Australia, Southern Africa and Europe, and *S. globosa* in Central America and parts of Eurasia. However, *S. brasiliensis* is known only from Brazil, where it is responsible for serious epidemic (Rodrigues *et al.* 2013, 2014). *Sporothrix luriei* is known based on only a single isolate from South Africa (Zhang *et al.* 2013, Teixeira *et al.* 2014).

#### Group D

*Sporothrix polyporicola* grouped alone in *Sporothrix* in our analyses (Fig. 5). This is consistent with the phylogenies of Osorio *et al.* (2016) and De Beer *et al.* (2016a).

#### Group E

In a similar manner, *S. polyporicola* and *S. phasma* grouped alone in *Sporothrix* in our analyses (Fig. 5). Both species were closely related in the LSU dataset of De Beer *et al.* (2016a).

#### Group F

Group F accommodated *S. nigrograna*, *S. curviconia*, *S. thermara*, *S. eucalyptigena* and *S. bragantina*. *Sporothrix thermara* and *S. bragantina* grouped together as “Lineage H” and *S. curviconia* as “Lineage G” in the phylogenies of De Beer *et al.* (2016a).

#### Group G

*Sporothrix dombeyi* formed a single lineage basal to *Sporothrix* in our concatenated dataset (Fig. 5). Previously *S. dombeyi* (as *O. nothofagi*) was transferred to *Sporothrix* and renamed by De Beer *et al.* (2016a). This species also grouped basal to *Sporothrix* in their datasets (along with other species treated here as Lineage XVI, XVIII, XIX).

#### New combination:

1) *Sporothrix longicollis* (Masse & E.S. Salmon) M. Procter & Z.W. de Beer, **comb. nov.** MycoBank MB 841005.  
*Basionym:* *Spumatoria longicollis* Masse & E.S. Salmon, Ann. Bot. 15: 351. 1901. MycoBank MB 171713.

*Description:* Masse & Salmon (1901: 350–351, fig. 27), Giraldo *et al.* (2017: 344–345, fig. 9).

*Phylogenetic data:* Giraldo *et al.* (2017).

*Notes:* *Sporothrix longicollis* is different from other *Sporothrix* spp. by having 1-septate ascospores, pale-coloured ascospores and coprophilous biology. The inclusion of this species in *Sporothrix* was also suggested by Giraldo *et al.* (2017).

### *Sporothrix incertae sedis* (Lineages XVI & XIX)

#### *Sporothrix fumea* (Lineage XVI)

*Sporothrix fumea* grouped basal to all the above-mentioned lineages in the analyses of our combined dataset (Fig. 5). In the phylogenies of De Beer *et al.* (2016a), *S. fumea* formed a lineage with *O. valdivianum* (Lineage XVIII), but in our phylogenies these species grouped separately.

#### *Sporothrix brunneoviolaceae* (Lineage XIX)

In the phylogenies of De Beer & Wingfield (2013), *S. brunneoviolaceae* formed a distinct lineage in *Ophiostoma* s.l. with

*S. fumea* and *O. fasciatum* but these were not available for the present study. However, this species grouped basal to *Sporothrix* in the phylogenies of De Beer *et al.* (2016a). In the analyses for the present study, *S. brunneoviolaceae* consistently grouped separately from *Sporothrix*.

## CONCLUSIONS

The results of this study have provided support for the delineation of most of the genera that have been recognised during the course of the last decade in the *Ophiostomatales*. This study also revealed robust novel lineages described here in four new genera. In addition to phylogenetic support, most of these genera include coherent groups of species that are characterised by similar morphology, ecology and/or geographical origin. The study has also resolved remaining One Fungus-One Name issues that were not dealt with in the revision of De Beer & Wingfield (2013). This is especially by providing new combinations for several species in *Grosmania* and *Leptographium*.

This study is the most extensive and most comprehensive ever undertaken on the taxonomy of the *Ophiostomatales*. The concatenated dataset included 264 taxa representing all major lineages in the Order. It was not possible to resolve the taxonomic status of some smaller lineages. These lineages may represent new genera or reside in existing genera that will emerge as new species are discovered. We have consequently chosen to retain species in these lineages in their current genera until such data can provide clarity on their taxonomic placement.

The phylogenies generated in this study will serve as a framework for future taxonomic studies on the *Ophiostomatales*. In the short term, they will facilitate the appropriate generic placement of novel species. But they will also provide the required lists of the appropriate species to include in smaller phylogenies of single genera and/or species complexes that will make it possible to confirm whether studied isolates represent novel taxa.

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## DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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**Fig. S1.** Phylogenetic tree derived from maximum likelihood analysis of the LSU gene region. The dataset consisted of 233 isolates and 859 characters before and after Gblocks treatment. Bootstrap values above 60 % are shown. Purple blocks indicate existing genera, yellow blocks new genera described in this study, green blocks genera that we redefine here, and blue blocks indicate genera that we here re-instate and re-define.

**Fig. S2.** Phylogenetic tree derived from maximum likelihood analysis of the ITS gene region. The dataset consisted of 235 isolates and 169 characters after Gblocks treatment (1 171 characters prior to Gblocks, including gaps). ML values above 60 % are shown. Purple blocks indicate existing genera, yellow blocks new genera described in this study, green blocks genera that we redefine here, and blue blocks indicate genera that we here re-instate and re-define.

**Fig. S3.** Phylogenetic tree derived from maximum likelihood analysis of the *TEF1-α* gene region. The dataset consisted of 207 isolates and 380 characters after Gblocks treatment (655 characters prior to Gblocks, including gaps). ML values above 60 % are shown. Purple blocks indicate existing genera, yellow blocks new genera described in this study, green blocks genera that we redefine here, and blue blocks indicate genera that we here re-instate and re-define.

**Fig. S4.** Phylogenetic tree derived from maximum likelihood analysis of the *RPBII* gene region. The dataset consisted of 171 isolates and 952 characters after Gblocks treatment (1 108 characters prior to Gblocks, including gaps). ML values above 60 % are shown. Purple blocks indicate existing genera, yellow blocks new genera described in this study, green blocks genera that we redefine here, and blue blocks indicate genera that we here re-instate and re-define.

**Table S1.** Taxa included in the phylogenomic analyses and their genome sequence statistics