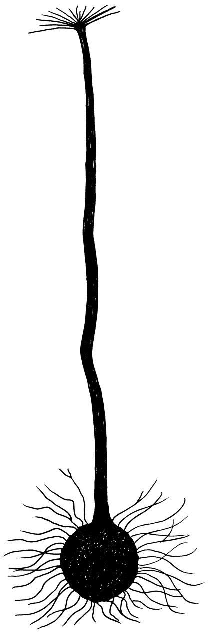
Taxonomy and phylogeny of *Ophiostoma* spp. with *Sporothrix* anamorphs and their generic relationships in the *Ophiostomatales*



Z. Wilhelm de Beer

Taxonomy and phylogeny of *Ophiostoma* spp. with *Sporothrix* anamorphs and their generic relationships in the *Ophiostomatales*

by

Z. Wilhelm de Beer

submitted in partial fulfilment of the requirements for the degree

Philosophiae Doctor

in the Faculty of Natural and Agricultural Sciences
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Supervisor: Prof. Michael J. Wingfield

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Declaration

I declare that the dissertation/thesis, which I hereby submit for the degree *Philosophiae Doctor* at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Z. Wilhelm de Beer 1 August 2012

Contents

Acknowledgements

Acknowledgements

I have postponed the writing of these acknowledgements to the absolute last minute before submitting the thesis, simply because, after a long PhD journey, it is very difficult to decide where to start. But the truth is I have given the acknowledgements much thought over the past few weeks, and have caught myself several times becoming extremely emotional, which is probably another reason why I evaded the writing thereof.

The fact is that a venture of this nature (i.e. the PhD) is probably one of the best examples of symbiosis there is. There is no way that one person can accomplish or survive this expedition on his or her own. But similar to so many of the bark beetle-fungus interactions we study, the symbiotic associations between the student and the biome in which he operates, can be extremely variable and complex. E.g. I thought of dividing the people I want to thank in two groups, family and friends, versus my colleagues, but I soon realized that in my life there is no clear separation between these groups. And then, as is the case in the life span of a bark beetle gallery, relationships change over time. Some people who played an important role 10 years ago when I started, is not around anymore, and during this the period other, new relationships developed. Some relationships with the same people also changed over time. However, there were two relationships during this period without which I would not have survived and the life cycle of this PhD would not have been completed.

Firstly, Sonja, my wife. This is a permanent, obligate relationship that also went through different phases. The first period was that of parasitism, where I, as a full-time student, was completely dependent on her. Later, when I got a permanent appointment, it changed to some form of commensalism, where I was still the beneficiary, but the effect on her was less detrimental. I would like to think that we are now entering a fully mutualistic phase, where both partners contribute and gain equally. Nevertheless, the following statement is no cliché: without Sonja’s love, physical and emotional support this thesis would not have been completed. Her support manifested in various ways from driving kids around, earning an income, prayers, sms’s of support, the delivery of snacks at my office at unexpected times, attending social events without me, and many more. Sonja, I love you, I appreciate every bit of what you have done for, and have been to me, and hope that I will somehow, some day, be able to return your grace.

The second obligate relationship, which I think was more of a commensal relationship from the start, was that with my primary and only supervisor, Mike. Mike, thank you for not losing faith in me, for your encouragement and wisdom,

and for releasing me from FABI duties during the past couple of months, so I could focus. Hopefully, also this relationship will turn out to become fully mutualistic.

I have decided not to expand from here onwards on the allegory with bark beetle-fungus symbiosis, because some non-biologists on this list might be offended if I compare them to a pathogen, a mite, a parasitic fungus, a nematode or perhaps some gut bacterium. But all of the following people played some role in the symbiosis, and I thank them for that:

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My Father and late Mother, for allowing me to become a biologist after all. And my sisters, mother-in-law, and other family for their love and support over the years.

And finally Zach, Petro and Marthinus, for whom I did this. I will really try to spend a bit more time with you now!

Lastly, I have to admit that there were times where I just did not have the energy and strength to sit down and write more! But somehow, I often experienced that the will and strength to continue came from elsewhere, outside of myself. I believe that these were the times when Sonja’s and others’s prayers were answered and where a graceful God stepped in and supplied what was lacking.

Preface

Preface

The ascomycete genus, *Ophiostoma* together with its sister genera in the *Ophiostomatales*, comprise more than 300 known species. Many of these fungi cause sap stain on freshly exposed sapwood and have a significant negative economic impact on timber companies globally. The majority of species are vectored by bark- or sapwood-infesting beetles (Scolytinae), or other arthropods such as mites. Although only a few species of *Ophiostoma sensu lato* are serious tree pathogens, the impact of these has been dramatic.

The genus is perhaps best known as a result of the disastrous Dutch elm disease pandemics that killed millions of native elm trees in Europe and north America during the 20th century (Gibbs 1978). The causal agents of this disease are *Ophiostoma ulmi* and some closely related species that are vectored by *Scolytus* bark beetles (Webber 1990). At present there are several other on-going epidemics where these fungi are contributing to major losses of natural forests and plantations. These include the mountain pine beetle (*Dendroctonus ponderosae*) epidemic in the north western parts of North America where the range of the beetle is expanding northwards and to higher altitudes as the result of global warming (Hicke *et al.* 2006).

Another situation where bark beetles and their fungal associates have caused serious damage is where they have been introduced into new environments and where native trees have not developed natural resistance to them. An example here is the red turpentine beetle (*Dendroctonus valens*), that has been introduced with one of its fungal associates, *Leptographium procerum,* from North America into China, killing huge numbers of pine species native to east Asia (Yan *et al.* 2005). The consequence of these and similar epidemics is that ophiostomatalean species are considered as important quarantine pathogens in the world that need to be considered during the import and export of wood products and solid wood packaging.

Interestingly, the *Ophiostomatales* includes some opportunistic human and animal pathogens in the genus *Sporothrix* that are the causal agents of a disease known as sporotrichosis (De Lima Barros *et al.* 2011). Although sporotrichosis is not contagious, it often causes localized epidemics when high levels of inoculum are present on specific substrates. Probably the most extreme epidemics took place in South African gold mines during the first half of the last century. Wooden poles used to support the roofs of mine tunnels sustained growth of *Sporothrix schenckii*, which infected any small wounds on the labourers (Quintal 2000). The lack of antifungal compounds made treatment of the disease difficult, often resulting in the dissemination of the disease to other parts of the body via lymphatic vessels. At present, there is a new sporotrichosis epidemic that has been on-going in the densely populated parts of Buenos Aires for the past ten years. Cats have access to only small patches of infected soil in the city, picking up the spores in their claws and infecting other cats and humans with the fungus through scratches. Several hundred cases of the disease have already been reported (Schubach *et al.* 2008). However, globally the disease has also regained attention of researchers during the past two decades due to the appearance of a variety of serious mycoses, in several cases

leading to the death of immuno-compromised, most often HIV positive patients (Freitas *et al.* 2012).
It is against this background of tree, human and animal disease that the importance of the taxonomy of the *Ophiostomatales* becomes evident. Responsible diagnostics and remedial or preventative measures rely on a solid foundation of good taxonomy. The introduction of DNA based techniques in the 1990's to resolve taxonomic questions has had a major impact on fungal taxonomy as a discipline. We can now reliably distinguish between closely related species. E.g. several cryptic human pathogenic species in the *S. schenckii* complex have been described in recent years, and these differ from each other in their pathogenicity (Arrilaga-Moncrieff *et al.* 2009) and their susceptibility to antifungal compounds Marimon *et al.* (2008). This means that more accurate identifications will translate to more efficient treatment regimes. DNA sequences have also made it possible to determine to which genus or species a fungal isolate belongs, irrespective of whether we know the anamorph, teleomorph or for that matter any morphological state. The capacity to accurately identify fungi in this way, and the realisation that we do not need to rely on morphological characters to resolve complex taxonomic problems, culminated in radical changes to the International Code of Nomenclature for Algae, Fungi and Plants (ICN). These changes, loosely referred to as the "one fungus one name principles", to the Code were adopted by the 18th International Botanical Congress in Melbourne in July 2011. The application of these principles will result in many name changes in the foreseeable future, but will eventually bring much needed stability in fungal nomenclature.

The genus *Ophiostoma* was considered a synonym of *Ceratocystis* for most of the latter half of the 20th century, and together, species of these genera were referred to as the ophiostomatoid fungi. The confusion between these genera transgressed all levels of their taxonomy, from the ordinal down to species level. Some of the earliest DNA-based studies in the 1990's showed that *Ceratocystis* belonged in the *Microascales*, and that *Ophiostoma* belonged in an order of its own, the *Ophiostomatales.* Results of the AFTOL (Assembling the Fungal Tree of Life) project further elucidated the placement of these orders in the *Sordariomycetes*. In addition, several studies during the past twenty years addressed and resolved specific genus level questions within these groups. However, neither the *Ophiostomatales* nor the *Microascales* has been redefined since 1990, based on the available phylogenetic data and with the inclusion of all related genera. It is against this backdrop that the studies presented in this thesis were undertaken.

The **first chapter** of this thesis addressed the phylogenetic placement of the ophiostomatoid genera at the order and family levels. Sequences representing all orders and families in the *Sordariomycetes* were used as scaffold to which sequences of species representative of all the ophiostomatoid genera were compared. The resulting phylogenies enabled me to formally redefine the *Ophiostomatales* and *Ophiostomataceae*, and revealed a new family, the *Graphiaceae*, to accommodate species of *Graphium s.str.* in the *Microascales*.

In **chapter two** I focussed on the *Ophiostomatales* and the delineation of genera within this order. Several studies over the past years interrogated genus level questions in this order. However, these studies typically included between 20 and 70 species, usually representing only one or two particular genera. The focus of most of these studies was to resolve the phylogenetic placement of specific morphological groups of species. Over time, it became clear that especially anamorph morphology within the *Ophiostomatales* is very plastic, and that classifications based on these features did not necessarily reflect phylogenetic relatedness or distance between taxa. E.g. many species produce intermediate forms between synnematous and mononematous conidiomata. Another example is that of several species producing strictly sporothrix-like anamorphs, while others produce these anamorphs together with synnematous synanamorphs. I screened all available sequence data for all ophiostomatalean species in GenBank, which amounted to almost 8000 sequences. I carefully selected the most reliable ribosomal DNA sequences representing each species, and where possible, those of the ex-type strains, also considering the publications from which these sequences were published. I identified reliable sequences of altogether 266 species residing in the order, and analysed these in three different data sets. Analyses of these data resulted in several new lineages, many of which revealed species relations not previously recognized. Six genera and 18 species complexes were defined. The results were interpreted based on the “one fungus one name” principles. Because all lineages could not be equally well resolved, I suggested a conservative approach and made several recommendations as to how to deal with these taxa in the interim and until more robust phylogenies become available that can resolve the uncertain delineation of genera.

The last complete nomenclator for the ophiostomatoid fungi was published in 1993, and included 138 teleomorphic species. The delineation of genera based on phylogenetic analyses discussed in chapters one and two, and the application of “one fungus one name” principles to species in these genera, resulted in a need for an updated nomenclator for these fungi. In **chapter three** I present a nomenclator of all ophiostomatoid species, both anamorphic and teleomorphic. This included 596 valid species in 11 genera. This is not merely a list of names, but for each species all relevant taxonomic literature as well DNA sequence data, where available, were considered and cited to ensure a correct generic placement. Three genera were redefined, and 26 new combinations and one *nomen novum* were made.

Phylogenetic analyses in chapter two supported previous suggestions that the so-called *Sporothrix schenckii-Ophiostoma stenoceras* complex in *Ophiostoma sensu lato*, might represent a distinct genus. In **chapter four**, this question was addressed using a four gene phylogeny for all species previously suggested to belong to this complex. This included 35 species of *Ophiostoma* and 17 *Sporothrix* spp. The results confirmed that 32 of the species formed a monophyletic lineage that included *S. schenckii*, the type species of the genus *Sporothrix*. The emended Code allows for anamorph genera to be redefined to include teleomorphic species. *Sporothrix* was thus redefined and 19 new combinations were provided for species of *Ophiostoma*.

Between 1971 and 1998, three *Sporothrix* spp. were described from diseased *Eucalyptus* leaves. The unique morphology of septal pores prompted the description of a new genus, *Quambalaria*, in 2000 to accommodate these species. However, as the phylogenetic position of these taxa remained unclear, I employed DNA sequences in **chapter five** to determine their generic placement. The results confirmed that they represented a distinct genus, but also a new family in the *Microstromatales*, a basidiomycete order in the *Ustilaginomycetes*. However, the phylogenetic relationship of one of the species, *Q. pusilla*, remained unclear because no culture was available for this species.

During the last few years, several more isolates of *Quambalaria* from various hosts on four continents became available for study. Also, I obtained a dried culture of *Q. pusilla*, the species for which no living culture was available during the work for chapter five. In **chapter six** I thus identified 35 isolates of *Quambalaria* based on DNA sequences. In addition to the ITS region, I developed new basidiomycete-specific primers for the elongation factor 1α gene region, and showed that this region supports ITS in the delineation of closely related species of *Quambalaria*. The data resolved the identity of *Q. pusilla*, revealed a new species, and led to several new host and country reports of *Quambalaria* spp.

The chapters of this thesis resolved several higher order, generic and species level questions related to ophiostomatoid genera and species, especially those with sporothrix-like anamorphs. The thesis serves as a timely review and interpretation of DNA sequence data generated for these taxa over the past 20 years. It also represents the first comprehensive assessment of the impacts that the newly adopted one fungus one name principles in the Code will have on ophiostomatoid taxonomy. This study will hopefully serve as foundation for ophiostomatalean taxonomy and nomenclator during the course of the next few years.

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Chapter 1

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The ophiostomatoid fungi: their dual position in the Sordariomycetes

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Abstract

The almost century-long confusion regarding the taxonomy of the ophiostomatoid fungi has confounded definitions of the orders and families in which genera such as *Ophiostoma* and *Ceratocystis* were originally classified. In this study, we combined and re-analysed ribosomal LSU and SSU DNA sequences from several recent studies. The resulting phylogenetic trees showed that ophiostomatoid species belong to either the *Ophiostomatales* (Sordariomycetidae) or the *Microascales* (Hypocreomycetidae) in the Sordariomycetes. Based on these results, we have redefined the *Ophiostomatales* and its only family, the *Ophiostomataceae*, to accommodate the genera *Ophiostoma sensu lato* (including *Pesotum* and *Sporothrix*), *Ceratocystiopsis, Fragosphaeria*, *Leptographium s. l.* (including *Grosmannia*)*, Raffaelea sensu stricto,* and *Graphilbum*. Analyses in this study showed that the *Microascales* include the *Microascaeae, Halosphaeriaceae, Ceratocystidaceae*, *Gondwanamycetaceae,* and the newly erected family, the *Graphiaceae*. The *Ceratocystidaceae* accommodates *Ceratocystis s. l.* (including *Thielaviopsis* and *Ambrosiella*) and *Cornuvesica*. The *Gondwanamycetaceae* includes *Knoxdaviesia* (= *Gondwanamyces*) and *Custingophora*, and the *Graphiaceae* includes *Graphium s. str.* The latter genus was redefined to include what was previously referred to as the *G. penicillioides* complex. We treat *Sphaeronaemella* as *incertae sedis* in the *Microascales.* Five genera previously treated in the *Ophiostomatales* or *Microascales* were excluded from these orders. These were *Canariomyces*, *Klasterskya*, *Lanspora*, *Rhynchophoma* and *Spumatoria*. The status of *Chaetonaemospora*, *Mycorhynchella*, and *Sporendocladia* remains to be clarified.

The ‘Ophiostomatoid Fungi’ is a term of convenience that was proposed to refer to an unnatural group of fungi with similar teleomorph morphology that arose due to convergent evolution with insects. Most species produce either ascospores or conidia or both spore types in sticky drops on elevated structures, specifically adapted for arthropod dispersal. For more than a century these analogous morphological characters were considered congruent by taxonomists, resulting in much confusion in the literature. When it became evident, initially from biochemical characterization (Rosinski & Campana 1964, Smith *et al.* 1967, Jewell 1974, Weijman & De Hoog 1975, Harrington 1981, De Hoog & Scheffer 1984) and subsequently based on DNA sequence data (Berbee & Taylor 1992a), that these morphological traits have evolved several times in the Ascomycota, mycologists working with this group of fungi were presented with a dilemma. Previously it was acceptable to refer to this group by the preferred genus name of the period, whether it was *Ceratostomella* (Hedgcock 1906, Davidson 1942), *Ophiostoma* (Sydow & Sydow 1919, Nannfeldt 1932, Melin & Nannfeldt 1934, Siemaszko 1939, Von Arx 1952) or *Ceratocystis* (Bakshi 1951, Moreau 1952, Hunt 1956, Wright & Cain 1961, Griffin 1968, Olchowecki & Reid 1974, Upadhyay 1981). But how were they to refer to a group of fungi, representing phylogenetically distinct genera, but with a common morphology, taxonomic history, and similar ecology? The problem was addressed by the invention of the term 'ophiostomatoid' in the book ‘*Ceratocystis* and *Ophiostoma*: Taxonomy, Ecology and Pathogenicity,’ that was the result of a symposium held in 1990 in Germany on all aspects of the taxonomy and biology of these fungi (Wingfield *et al.* 1993). The title of the book, as well as the majority of its taxonomic content, recognized that *Ceratocystis* and *Ophiostoma* were indeed distinct, but the term made it possible to collectively refer to them as a group.

Interestingly, the *Ceratocystis* and *Ophiostoma* book (Wingfield *et al.* 1993) did not contain a single phylogenetic tree, only six of the 30 chapters mentioned DNA at all, and only one of these chapters presented DNA sequence data (Blackwell *et al*. 1993). The reason was that the book appeared at a time when the first DNA sequence data, confirming the phylogenetic separation of *Ophiostoma* and *Ceratocystis,* were just becoming available. Hausner *et al*. (1992) was the first to produce a phylogenetic tree for these fungi based on nuclear ribosomal small subunit (SSU) sequences. They showed a clear separation between *Ophiostoma* and *Ceratocystis* among some other Ascomycete genera. In the same year, the first ever paper appeared in which an anamorphic fungal species (*Sporothrix schenckii*) was placed in a teleomorph genus (*Ophiostoma*) (Berbee & Taylor 1992b). Soon afterwards, the first two papers appeared that conclusively placed *Ophiostoma* and *Ceratocystis* in respectively the *Ophiostomatales* and *Microascales* based on DNA sequence comparisons (Hausner *et al.* 1993d, Spatafora & Blackwell 1994). Several papers followed that addressed taxonomic questions with DNA sequence data at genus level (Hausner *et al.* 1993b, c, Wingfield *et al*. 1994, 1999, Visser *et al.* 1995, Blackwell & Jones 1997, Marais *et al.* 1998, Okada *et al.* 1998, Viljoen *et al.* 1999), as well as at the species level (Jeng *et al.* 1996, Issakainen *et al.* 1997, Strydom *et al.* 1997, Witthuhn *et al.* 1998, 1999). By 1995, the first paper appeared where a new ophiostomatoid species, *Ceratocystis albifundus*, was described based on internal transcribed spacer (ITS) sequences (Wingfield *et al.* 1996). But it was only after the dawn of the new millennium that DNA sequences became a routine feature in the descriptions of novel ophiostomatoid species (Coetsee *et al.* 2000, Barnes *et al.* 2003, Jacobs & Kirisits 2003, Aghayeva *et al.* 2004, Van Wyk *et al.* 2004, Zhou *et al*. 2004, etc.). To date, 82 new ophiostomatoid species have been described in the *Ophiostomatales*, and 48 in the *Microascales*, based on DNA sequence data.

If it is accepted that the authoritative 1993 book had already recognised that *Ceratocystis* was distinct from *Ophiostoma,* and the subsequent evidence provided by DNA sequences supported the placement of these and allied genera in two distinct orders of the Ascomycota, the question might be asked why these genera should still be treated in a single volume, let alone in one chapter? The answer to this question might be found in some numbers based on publications. We conducted online searches in SciVerse Scopus (www.info.sciverse.com/scopus) and the ISI Web of Knowledge (www.isiwebofknowledge.com), and counted the number of papers published each year since 1993, listing either *Ceratocystis,* or *Ophiostoma,* or those mentioning both genus names in the title, abstract or keywords (**Fig. 1**). If we assume that by 1993 the majority of mycologists and plant pathologists working with the ophiostomatoid fungi would have accepted that *Ceratocystis* and *Ophiostoma* were distinct, a significant decline in the number of papers mentioning both genus names would be expected. However, of the 953 papers published from 1993 to 2011 mentioning these genera, 167 (18%) listed both genus names. Of these, 36% had pathology (including all aspects of resistance) as main topic, 33% dealt with taxonomy, 17% with ecology (including symbiosis), 10% with sapstain, and 4% with population genetics. The overall trend over the study period was that the total number of papers on *Ceratocystis* and *Ophiostoma* published annually had increased (**Fig. 1a**), while the percentage of the total number of papers mentioning both genus names had decreased (**Fig. 1b**). However, the actual number of papers mentioning both genera has remained almost constant since 1993, averaging about nine per year (**Fig. 1c**). The numbers of species listed in the latest nomenclator (De Beer *et al.* 2012) are also informative. As a result of a century of taxonomic confusion, 109 valid species currently treated in the *Ophiostomatales* in *Ophiostoma, Grosmannia, Ceratocystiopsis* or *Graphilbum*, had at some stage or other been treated in *Ceratocystis,* while 10 valid *Ceratocystis* spp. had been treated at some point in *Ophiostoma*. Similarly, 15 *Ophiostoma* spp., five *Grosmannia* spp., five *Ceratocystis* spp. and one *Ceratocystiopsis* sp. had been treated in *Ceratostomella*. All future nomenclators, monographs or other taxonomic papers treating any of these species, will have to consider their homotypic synonyms. By definition, good taxonomy always considers its history, and for that reason *Ophiostoma*, *Ceratocystis* and *Ceratostomella* will forever be linked, even though DNA sequence data have irrefutably separated them. This is probably the reason why the number of annual publications mentioning both *Ceratocystis* and *Ophiostoma* remains more or less constant, and it also explains why we are still considering these genera and their relatives in a single chapter.

Over the past 20 years, several papers have addressed the phylogenetic placement and delineation of the ophiostomatoid genera *Ceratocystis* (Hausner *et al.* 1993d, Spatafora & Blackwell 1994), *Thielaviopsis* (Paulin-Mahady *et al*. 2002), *Gondwanamyces* (Wingfield *et al*. 1999), *Cornuvesica* (Hausner & Reid 2004), *Ambrosiella* (Massoumi Alamouti *et al*. 2009) and *Graphium* (Okada *et al.* 1998) within the *Microascales*, and that of *Ophiostoma*, *Grosmannia*, *Ceratocystiopsis* (Zipfel *et al.* 2006), *Fragosphaeria* (Suh & Blackwell 1999), *Leptographium* (Jacobs *et al.* 2001), *Pesotum* (Okada *et al.* 1998), *Sporothrix* (De Beer *et al.* 2003), and *Raffaelea* (Harrington *et al*. 2010) in the *Ophiostomatales*. Augmenting these studies, papers based on the data produced during the AFTOL project (Lutzoni *et al.* 2004) shed new light on the position of the two orders in the Ascomycota (Spatafora *et al.* 2006, Zhang *et al.* 2006, Hibbett *et al.* 2007, Schoch *et al.* 2007, 2009, Réblová *et al.* 2011). However, none of the above-mentioned studies included DNA sequences representative of all the currently accepted ophiostomatoid genera. The aim of the present investigation was thus to consider for the first time in a single study, the phylogenetic relationships of all the ophiostomatoid genera at the family and order levels within the Sordariomycetes, to facilitate an accurate delineation of both the *Ophiostomatales* and *Microascales*. We also considered and discuss all genera suggested over time to be related to ophiostomatoid genera in either of the two orders.

For as comprehensive an analysis of the ophiostomatoid genera as possible, the gene regions of choice were the ribosomal small subunit (SSU) and large subunit (LSU) regions, since data for these two loci were available for the largest number of species. Initially, we included all the available SSU and LSU sequences for species in the ophiostomatoid genera (data not shown). Through careful screening we then selected a limited number of sequences representing each genus. These sequences were aligned and analysed with the AFTOL and other reliable data representing all recognized orders within the Sordariomycetes as framework (Hibbett *et al.* 2007, Schoch *et al.* 2009), in two separate data sets representing the two gene regions. Data sets were assembled using MEGA 5 (Tamura *et al.* 2011). Alignment of data was done online using the FFT-NS-I strategy in MAFFT 6 (Katoh & Toh 2008). The most appropriate models for maximum likelihood (ML) analyses were selected using jModeltest 0.1.1 (Posada 2008), and for Bayesian inference (BI) using MrModeltest 2.3 (www.abc.se/~nylander/). ML was performed in PhyML 3.0 (Guindon *et al.* 2010) and maximum parsimony (MP) in MEGA 5, with node support in both cases determined using 1000 bootstrap replicates. For Bayesian Inference (BI) four MCMC searches were conducted in two simultaneous runs for 5 million generations, sampling every 100th iteration. BI was done using MrBayes 3.1.2 (Ronquist & Heulsenbeck 2003) and 'burnin' of each search was determined with Tracer 1.4 (www.tree.bio.ed.ac.uk/software/tracer/). Phylogenetic trees resulting from these analyses (**Figs 2, 3**) are discussed where appropriate in the sections below.

THE *OPHIOSTOMATALES* AND THE *OPHIOSTOMATACEAE*

The order *Ophiostomatales* was described by Benny & Kimbrough (1980) to accommodate a single family, the *Ophiostomataceae*, that was treated prior to 1980 in the *Plectascales* (Nannfeldt 1932), *Microascales* (Luttrell 1951, 1955), *Sphaeriales* (Ainsworth & Bisby 1954, Von Arx 1979), and as a synonym of the *Endomycetaceae* in the *Endomycetales* (Redhead & Malloch 1977). The family *Ophiostomataceae* was described long before the order (Nannfeldt 1932) and its initial definition included *Ophiostoma,* with *Ceratostomella* and *Endoconidiophora* as synonyms. Alongside *Ophiostoma*, Goidànich (1936) added *Grosmannia*, *Ophiostomella*, and *Chaetoceratostoma* to the family, while Gäumann (1952) included *Microascus*. From the early 1950's onwards, *Ophiostoma* was considered a synonym of *Ceratocystis* by most authors (Bakshi 1951, Moreau 1952, and others), with *Ceratocystis* often being treated in the *Ophiostomataceae* (Davidson 1958, Rosinski 1961, Ainsworth 1963, 1971, Kendrick & Molnar 1965). Müller & Von Arx (1973) listed *Europhium* and *Sphaeronaemella* together with *Ceratocystis* in the family, and Upadhyay & Kendrick (1975) added *Ceratocystiopsis*. When Benny & Kimbrough (1980) eventually described the *Ophiostomatales,* they accepted the *Ophiostomataceae* as the only family in the new order, including four genera: *Ceratocystis, Ceratocystiopsis*, *Ophiostoma*, and *Sphaeronaemella.* Upadhyay (1981), apparently unaware of the Benny & Kimbrough (1980) paper, redescribed the *Ophiostomataceae* and designated *Ceratocystis* as the type genus, with *Ophiostoma, Sphaeronaemella, Grosmannia* and *Europhium* as its synonyms, and with *Ceratocystiopsis* as a second genus in the family and order. The only two formal family descriptions published since Upadhyay (1981), correctly excluded *Ceratocystis* from the *Ophiostomataceae,* but treated *Ophiostoma, Europhium*, and *Ceratocystiopsis* as distinct genera (Von Arx & Van der Walt 1987, Barr 1990). For some years, the latter two were treated as synonyms of *Ophiostoma* (Wingfield 1993, Hausner *et al*. 1993b), until Zipfel *et al.* (2006) re-instated *Ceratocystiopsis* and *Grosmannia* (with *Europhium* as synonym) alongside *Ophiostoma* in the *Ophiostomatales*. Hausner *et al.* (1993c), Spatafora & Blackwell (1994), and several subsequent authors showed that *Ceratocystis* was 'best disposed in the *Microascales',* which implied that the *Ophiostomatales* should be typified by *Ophiostoma*. Although the order and family were appropriately treated by Kirk *et al.* (2008), neither of the two had been redefined since Barr (1990). Considering the confusion in the delineation of the *Ophiostomatales* and the *Ophiostomataceae* as described above, and the dramatic changes in the taxonomy of the ophiostomatoid fungi during the past two decades, it is clear that the circumscriptions of the family and order are in need of revision accommodating the clarity that DNA sequence analyses provide.

The phylogenetic position of the *Ophiostomatales* and its status as distinct order in the sub-class *Sordariomycetidae* was confirmed in multigene phylogenies (Zhang *et al.* 2006, Schoch *et al.* 2007, 2009) that were an outcome of the AFTOL project (http://www.aftol.org/). Phylogenetic trees (**Figs 2, 3**) resulting from our analyses included selected species of all the major groups in the *Ophiostomatales,* and supported the lineages revealed in the more comprehensive phylogenies of the *Ophiostomatales* constructed by De Beer & Wingfield (2012, Figs 1, 2). Central to the *Ophiostomatales* is the lineage representing *Ophiostoma s. str.* (**Figs 2, 3**) that contains the type species for the genus, *O. piliferum* (Sydow & Sydow 1919). *Ophiostoma s. str.* also includes several species complexes discussed comprehensively by De Beer & Wingfield (2012), and forms part of a larger, less well defined contingent defined as *Ophiostoma s. l.* The latter at present includes species complexes like the *Sporothrix schenckii-O. stenoceras* complex, the generic status of which needs reconsideration.

The second major group in the *Ophiostomatales* was defined as *Leptographium s. l.* by De Beer & Wingfield (2012), who showed that this group is not monophyletic as previously suggested (Zipfel *et al.* 2006). The type species for *Leptographium* and *Grosmannia*, namely *L. lundbergii* and *G. penicillata* respectively, separate in two distinct lineages within this group. As is the case for *Ophiostoma s. l.*, the generic status of these two lineages and several other species complexes in *Leptographium s. l.* needs reassessment.

The remaining four genera in the *Ophiostomatales*, *Fragosphaeria, Raffaelea s. str.*, *Ceratocystiopsis*, and the newly resurrected *Graphilbum*, are all delineated and discussed by De Beer & Wingfield (2012). The association of both *Ceratocystiopsis* and *Graphilbum* with *Ophiostoma* and the *Ophiostomatales* were evident since the inception of these genera (Upadhyay & Kendrick 1975). However, the both *Fragosphaeria* and *Raffaelea* had been treated elsewhere prior to their inclusion in the *Ophiostomatales*. The cleistothecial genus *Fragosphaeria* was previously treated in the families *Cephalotheceae* (Von Höhnel 1917, Nannfeldt 1932, Benny & Kimbrough 1980) and *Pseudeurotiaceae* (Malloch & Cain 1970, Fennell 1973) as part of the *Eurotiales* (Benny & Kimbrough 1980). Von Arx (1987) treated the *Pseudeurotiaceae* in the *Sphaeriales*, rather than the *Eurotiales*. *Raffaelea*, being a genus of only asexual ambrosial species, was treated by Batra (1967) in the *Tuberculariaceae*. The latter was a family in the *Tuberculariales*, one of the four orders in which the Hyphomycetes were traditionally divided (Kirk *et al.* 2008). Von Arx & Van der Walt (1987) were the first to list *Raffaelea* as one of the anamorph genera in the *Ophiostomataceae*. Our results confirmed the placement of *Fragosphaeria* and *Raffaelea* in the *Ophiostomatales* by respectively Suh & Blackwell (1999) and Jones & Blackwell (1998).

For the present we treat *Ophiostoma s. l.*, *Leptographium s. l.*, *Ceratocystiopsis*, *Fragosphaeria*, *Raffaelea* and *Graphilbum* in the *Ophiostomataceae.* Until the generic status of the unresolved lineages within the Ophiostomatales is determined using multigene data, we prefer not to introduce new families in the order. For the present, the *Ophiostomataceae* is thus maintained as the only family in the order. The last formal descriptions for the order and family were published prior to the availability of DNA sequence data. We, therefore, emend the descriptions of the *Ophiostomatales* and *Ophiostomataceae* to reflect current perspectives (**Box 1**).

OPHIOSTOMATOID FAMILIES AND GENERA IN THE *MICROASCALES*

The *Microascales* and *Microascaceae* were described by Luttrell (1951), albeit invalidly, to accommodate *Microascus.* He included the *Ophiostomataceae* as a second family in the order, and considered *Ceratocystis* a synonym of *Ophiostoma*. Malloch (1970) validated the *Microascaceae* with *Microascus* as type genus. Benny & Kimbrough (1980) followed by validating the *Microascales*, and recognising the *Microascaceae, Chadefaudiellaceae* and *Pithoascaceae* in the order. However, they excluded *Ceratocystis* from the *Microascales,* and treated it with *Ceratocystiopsis*, *Sphaeronaemella*, and *Ophiostoma*, in the *Ophiostomatales*. Von Arx & Van der Walt (1987) treated *Ceratocystis* in the *Lasiosphaeriaceae* (*Sordariales*), while Barr (1990) treated it in the *Pyxidiophoraceae* (*Hypocreales*). Hausner *et al.* (1993c, d) and Spatafora & Blackwell (1994) were the first to confirm the separation of *Ophiostoma* from *Ceratocystis* at ordinal level based on DNA sequences, placing the latter genus in the *Microascales*. Subsequent phylogenetic studies suggested the placement of six additional ophiostomatoid genera within the *Microascales*. These included *Sphaeronaemella* (Spatafora & Blackwell 1994)*, Ambrosiella* (Cassar & Blackwell 1996), *Graphium* (Okada *et al.* 1998), *Gondwanamyces* (Wingfield *et al.* 1999)*, Custingophora* (Viljoen *et al*. 1999), and *Cornuvesica* (Hausner & Reid 2004). Several of these and other phylogenetic studies, including multigene phylogenies, showed that these genera form lineages within the *Microascales* that are distinct from the lineage containing *Microascus* and its allied genera (Spatafora *et al.* 1998, Paulin & Harrington 2000, Réblová & Winka 2000, Hausner & Reid 2004, Huhndorf *et al.* 2004, Réblová & Seifert 2004, 2007, Zhang *et al.* 2006, Schoch *et al.* 2007, 2009, Tang *et al.* 2007, Sakayaroj *et al.* 2011, Réblová *et al*. 2011). Réblová *et al*. (2011) defined two of these lineages as new families, namely the *Ceratocystidaceae* and the *Gondwanamycetaceae*, alongside the *Microascaceae* and *Halosphaeriaceae*. They concluded that the status of the fifth family, the *Chadefaudiellaceae,* until recently listed under the *Microascales* (Kirk *et al.* 2008), is uncertain since no sequence data are available for its exemplar genus, *Chadefaudiella*.

Similar to the situation in the *Ophiostomatales*, the last full descriptions of the *Microascales* and *Microascaceae* were published by Barr (1990), and have become outdated for reasons set out above. However, there is one reason to apply caution before the description of the order can be emended. In some publications genera currently treated in the *Microascales* did not form a well-supported lineage in phylogenetic trees based on LSU data (Tang *et al.* 2007, Kolařík & Hulcr 2009, Réblová *et al.* 2011), suggesting that the *Microascales* might not be monophyletic. However, results from SSU data from the same studies showed a monophyletic lineage with good support. This support was also exhibited in SSU trees from other studies (Spatafora *et al.* 1998, Jacobs *et al.* 2003, Hulcr *et al.* 2007), as well as in multigene trees obtained from combined data of three (Schoch *et al.* 2007, Réblová *et al.* 2011, Sakayaroj *et al.* 2011), four (Zhang *et al*. 2006), five (Spatafora *et al*. 2006), and six gene regions (Schoch *et al.* 2009). We are convinced that these studies have provided sufficient evidence to confirm the monophyly of the *Microascales*.

In our re-assessment of the *Microascales*, we included all available SSU and LSU rDNA sequence data for the ophiostomatoid species known to be associated with this order. We used the same reference data as for analyses of the *Ophiostomatales*. Our results confirmed the phylogenetic position of the *Microascales* and its status as a distinct order in the sub-class *Hypocreomycetidae* as was revealed by the multigene phylogenies resulting from the AFTOL project (Zhang *et al.* 2006, Schoch *et al.* 2007, 2009). The resulting LSU trees (**Fig. 2**) reflected the split in the *Microascales* as was present in the studies mentioned above, while the SSU tree (**Fig. 3**) supported the monophyly of the order. Both data sets produced six well-supported lineages within the *Microascales* (**Figs 2, 3**). Five of these lineages included ophiostomatoid species (species names in bold type, **Figs 2, 3**), and four lineages corresponded to recognized families. Several *Graphium* spp. constituted the fifth distinct lineage, while *Sphaeronaemella* spp. formed a sixth lineage. Each of these lineages is considered separately below.

The *Microascaceae*

In his validation of the *Microascaceae*, Malloch (1970) included the genera *Microascus, Kernia*, *Lophotrichus*, *Petriella* and *Petriellidium* in the family. Von Arx (1973) added *Pithoascus,* Locquin-Linard (1977) *Enterocarpus,* and Von Arx (1978) *Faurelina,* but Benny & Kimbrough (1980) erected a separate family, the *Pithoascaceae*, for *Pithoascus* and *Faurelina*. McGinnis *et al*. (1982) synonymized *Petriellidium* with *Pseudallescheria*. Barr (1990) included *Pseudallescheria* with all the genera listed above, apart from *Faurelina*, in the *Microascaceae*. The first study in which DNA sequences of the *Microascaceae* were published, placed *Microascus* and *Pseudallescheria* together in the family (Berbee & Taylor 1992a). Subsequent studies confirmed the inclusion of additional teleomorph genera in the *Microascaceae*: *Kernia* (Hausner *et al.* 1993c), *Petriella* (Issakainen *et al.* 1997), *Lophotrichus* and *Petriellopsis* (Gilgado *et al.* 2007). The inclusion of *Lophotrichus* confirmed the synonymy of the *Lophotrichaceae* (Seth 1971) with the *Microascaceae*, as was suggested earlier by Eriksson (1982). Issakainen *et al.* (2003) placed the type species of *Pithoascus* in *Microascus*, confirming the synonymy of these two genera as proposed by Abbott *et al.* (2002) based on morphology. This implied that the *Pithoascaceae* should be treated as a synonym of the *Microascaceae* (Kirk *et al.* 2008). An unpublished sequence for *Enterocarpus grenotii* (CBS 380.78) in GenBank, grouped in our analyses (**Fig. 2**) with *Kernia* spp., suggesting that *Enterocarpus* indeed belongs in the *Microascaceae* as was suggested by Locquin-Linard (1977), but this needs confirmation with sequences for *E. unisporus,* the type species of the genus. Of all the teleomorph genera suggested to belong in the *Microascaceae* before DNA sequences were available, *Faurelina* is the only one that is now excluded from the family (Réblová *et al*. 2011).

Based on DNA sequences, several anamorph genera could be linked to teleomorph genera in the *Microascaceae*, e.g. *Scedosporium* with *Pseudallescheria* (Issakainen *et al*. 1997), and *Scopulariopsis, Doratomyces, Trichurus,* and *Wardomyces* with *Microascus* (Issakainen *et al*. 1999). A new anamorph genus, *Parascedosporium*, was recently described (Gilgado *et al.* 2007) to accommodate *Graphium tectonae,* a species typically considered with the ophiostomatoid fungi (Seifert & Okada 1993). Lackner & De Hoog (2011) subsequently showed that *Parascedosporium tectonae* is a synonym of another, older species, *Graphium putredinis,* that previously also has been treated with the ophiostomatoid fungi (Seifert & Okada 1993). The name *Parascedosporium putredinis* (**Figs 2, 3**) should thus be used preferentially for this species, which has consequently become the type species for *Parascedosporium* (Lackner & De Hoog 2011). Although much progress has been made in the delineation of genera within the *Microascaceae* (Rainer & De Hoog 2006, Gilgado *et al.* 2007, Lackner & De Hoog 2011), the status of the lineage containing *Scedosporium prolificans* (Lackner & De Hoog 2011) and several lineages within *Microascus* (Issakainen *et al.* 2003) still needs clarification, especially in view of the current move towards one fungus one name (Hawksworth 2011a). The *S. prolificans* lineage probably represents a distinct genus, for which the name *Lomentospora* would be available (Hennebert & Desai 1974, Gueho & De Hoog 1991, Lennon *et al*. 1994).

Phylogenetic data has changed the concept of the *Microascaceae* as defined by Barr (1990). For example, she included *Graphium* in her definition, which implies that the family needs to be redefined. However, since the taxonomy of genera and species in this family is beyond the field of expertise of the authors of the present chapter, we prefer not to emend the description at this stage.

The *Halosphaeriaceae*

The *Halosphaeriaceae* is the only family in the *Microascales* that does not include any ophiostomatoid fungi, and unlike its terrestrial counterparts in the order, all species in this family are saprobic on decaying plant material in aquatic habitats (Spatafora *et al*. 1998).

The family was invalidly described by Müller & Von Arx (1962), and validated by Kohlmeyer (1972), who treated it in the *Sphaeriales*. Eriksson (1984) assigned the *Halosphaeriaceae* as a single family to the *Halosphaeriales*, that he described invalidly. The order was validated by Hawksworth & Eriksson (1986). The first phylogenetic study using DNA sequences for this group (Spatafora *et al*. 1998), showed that the order was polyphyletic, with the major lineage grouping sister to the *Microascales*. A second, smaller lineage grouped further away and was later described as a distinct order, the *Lulworthiales* (Kohlmeyer *et al.* 2000). Despite the fact that several subsequent studies showed that the major lineage of halosphaerialean genera was actually derived from within the *Microascales* (Kong *et al.* 2000, Zhang *et al.* 2006, Schoch *et al.* 2007, Tang *et al.* 2007, Jones *et al.* 2009), it was only recently that the order was reduced to synonymy with the *Microascales*, and the *Halosphaeriaceae* treated as a family within the latter order (Hibbett *et al.* 2007, Kirk *et al*. 2008, Schoch *et al*. 2009, Réblová *et al*. 2011, Sakayaroj *et al*. 2011). Our analyses support its status as distinct family within the *Microascales* (**Figs 2, 3**). To the best of our knowledge, the original description of the *Halosphaeriaceae* (Kohlmeyer 1972) is the only formal description to date. Although several keys to the 53 genera in the family have been published (Jones 1995, Jones *et al*. 2009, Sakayaroj *et al*. 2011), an emended description for the family is needed, as well as a re-evaluation of the status of all genera considering the one fungus one name principles (Hawksworth 2011a). Since the *Halosphaeriaceae* does not include any of the ophiostomatoid fungi, we would rather not discuss the genera in this family individually in the present review, nor provide a redescription of the family.

The *Ceratocystidaceae*

In some earlier studies, the lineage in the *Microascales* that included *Ceratocystis, Ambrosiella* and *Cornuvesica* (**Figs 2, 3**) was referred to as *incertae sedis* (Kong *et al.* 2000, Tang *et al.* 2007, Sakayaroj *et al.* 2011), the '*Ceratocystis* group' (Réblova & Seifert 2004), or merely treated as part of the *Microascales* (Spatafora *et al*. 1998, Zhang *et al*. 2006, Schoch *et al*. 2007, 2009, Réblova & Seifert 2007). *Ceratocystis* is the oldest and largest genus in this lineage (**Figs 2, 3**), which includes *C. fimbriata*, type species for the genus. *Ceratocystis* is thus the preferred genus from which to derive a family name for this lineage. Locquin (1972) described a family with *Ceratocystis* as type genus, incorrectly as the '*Ceratocystaceae*' (see Art.18.1 & 18.4, McNeill *et al.* 2006) and without a Latin diagnosis, rendering it invalid. Although several subsequent authors made reference of this family (Locquin 1974, Wehmeyer 1975, Eriksson 1982, 1984, Kirk *et al.* 2001, 2008, Harrington 2004, Benjamin *et al.* 2004) using various spellings (*Ceratocystaceae*, *Ceratocystidaceae*, *Ceratocystiaceae*), the name was only recently validated by Réblová *et al*. (2011). The *Ceratocystidaceae* accommodates *Ceratocystis, Cornuvesica*, *Thielaviopsis* and *Ambrosiella* (**Figs 2, 3**).

The genus *Ceratocystis s. l.*, treated in depth by Wingfield *et al.* (2012), includes at least four well-defined lineages, namely *C. fimbriata s. l., C. moniliformis s. l.*, *C. coerulescens s. l.* and *Thielaviopsis*. These lineages represent distinct genera in the *Ceratocystidaceae* in the process of being described (Wingfield *et al.* 2012).

The genus *Cornuvesica* was established by Viljoen *et al.* (2000) to accommodate *Ceratocystiopsis falcata* (Upadhyay 1981), initially described as *Ceratocystis falcata* (Wright & Cain 1961). Based on its phylogenetic position (Hausner & Reid 2004), similarities with *Ceratocystis* in anamorph morphology, and its wood-inhabiting (Wright & Cain 1961, Rayner & Hudson 1977), bark-beetle associated ecology (Hutchison & Reid 1988), we treat *Cornuvesica* with *Ceratocystis* in the *Ceratocystidaceae.* However, the distinctive teleomorph morphology of *Cornuvesica*, possible mycoparasitic activity (Rayner & Hudson 1977, Hutchison & Reid 1988, Kawchuk *et al.* 1993), and relative phylogenetic distance from *Ceratocystis*, support the separation of the two genera.

The ambrosial genus *Ambrosiella* was represented in our analyses by its type species*, A. xylebori,* and *A. ferruginea* (**Figs 2, 3**)*.* Earlier phylogenetic studies showed that *Ambrosiella* species formed two groups, some species grouping with *A. xylebori* in the *Microascales,* and the remaining species in the *Ophiostomatales* (Cassar & Blackwell 1996, Blackwell & Jones 1997, Gebhardt *et al.* 2005). The species in the *Ophiostomatales* were transferred to *Raffaelea* and *Hyalorhinocladiella* by Harrington *et al.* (2010) and are discussed by De Beer & Wingfield (2012). Massoumi Alamouti *et al*. (2009) showed that the three *Ambrosiella* spp. in the *Microascales* separate in two lineages. Six *et al*. (2009) described a fourth species, which grouped in one of these lineages with *A. xylebori* and *A. hartigii,* close to *Ceratocystis adiposa*. *A. ferruginea* did not group with any other species, but was close to *C. fagacearum* (Six *et al*. 2009). The differences in beta-tubulin intron arrangement between these two groups and *Ceratocystis* species (Six *et al.* 2009), suggest a serious reconsideration of the generic status of these lineages together with the groups in *Ceratocystis* distinguished by Wingfield *et al.* (2012). The phylogenetic position of *A. trypodendri*, currently treated in *Ambrosiella* based only on conidiogenesis, remains to be determined because no DNA sequences are available for the species (Harrington *et al.* 2010).

The *Gondwanamycetaceae*

The genus *Gondwanamyces* was established to accommodate *Ceratocystiopsis proteae* and *Ophiostoma capense*, both species known only from *Protea* infructescences in South Africa (Marais *et al.* 1998). The genus was erected based on the phylogenetic relatedness of *Cop. proteae* (Hausner *et al.* 1993b, c) and *O. capense* (Marais *et al.* 1998, Wingfield *et al.* 1999) to each other, and with *Ceratocystis,* in the *Microascales.* The anamorphs of these two species were initially placed in the genus *Knoxdaviesia* (Wingfield *et al*. 1988, Wingfield & Van Wyk 1993). However, Viljoen *et al.* (1999) showed that *Custingophora olivaceae,* type species for the genus *Custingophora* (Stolk & Hennebert 1968), is phylogenetically related to *Gondwanamyces* and morphologically similar to the *Knoxdaviesia* anamorphs of *Gondwanamyces.* Réblová & Winka (2000) suggested that *Knoxdaviesia* be considered a synonym of *Custingophora*. Kolařík & Hulcr (2009) provided the necessary new combinations in *Custingophora* for the anamorphs of the two species from *Protea*, and described two additional species, one in *Gondwanamyces* and the other in *Custingophora*. In the most recent study on this group of fungi, Van der Linde *et al.* (2012) described an additional two *Gondwanamyces* species from *Euphorbia* in South Africa. Both these species are known only by their anamorphs. They furthermore suggested that *Custingophora* represents a genus distinct from *Gondwanamyces,* with *Cu. olivaceae* as its only known species. *Custingophora cecropiae* was thus transferred to *Gondwanamyces*. However, based on the one fungus one name principles (Hawksworth 2011a), *Knoxdaviesia* as the older name has priority over *Gondwanamyces*. De Beer *et al.* (2012) thus redefined *Knoxdaviesia* to include sexual states and provided new combinations where needed.

In our analyses, *Knoxdaviesia* and *Custingophora* species formed a lineage sister to the *Ceratocystidaceae* (**Figs 2, 3**). Results from several studies previously also showed that *Gondwanamyces* isolates, although related to *Ceratocystis*, formed a very distinct, well-supported lineage (Wingfield *et al.* 1999, Kolařík & Hulcr 2009, Schoch *et al*. 2009). In their circumscription of families within the *Microascales*, Réblová *et al*. (2011) maintained that there is sufficient phylogenetic distance between the *Ceratocystidaceae* and the lineage containing *Gondwanamyces* (now *Knoxdaviesia*) and *Custingophora* to justify the description of a new family for this group, the *Gondwanamycetaceae*. The latter name remains valid even though *Gondwanamyces* is currently treated as synonym of *Knoxdaviesia*.

Goidanichiella

Jacobs *et al.* (2005) placed the type species of the genus *Goidanichiella* based on SSU sequences in the *Microascales* with *Ceratocystis fimbriata, Cu. olivacea,* and *Go. proteae.* The sequence is unfortunately not in a public database, so the species was not included in our analyses. Kolařík & Hulcr (2009) suggested that *Goidanichiella* is a synonym of *Custingophora* because of morphological similarities, but Réblová *et al.* (2011) preferred to treat them as distinct based on the presence of *Aspergillus*-like vesicles on conidiophores of *Goidanichiella* spp. The inclusion of *G. barronii* in the *Microascales* (Jacobs *et al.* 2005) was probably correct, although the small number of taxa in their study prevented an accurate placement within the order. However, the morphological similarities between *Goidanichiella* and *Custingophora* spp. suggest that the two genera are closely related and that *Goidanichiella* might belong in the *Gondwanamycetaceae*. *Goidanichiella* and all four its known species were invalid until recently as a result of nomenclatural technicalities, but these have been corrected and the genus and species validated (Gams *et al*. 1990, 2009). Any future treatment of the *Gondwanamycetaceae* should thus include the species of *Goidanichiella* to resolve the uncertainty obscuring its generic status.

The *Graphiaceae*, a new family for *Graphium s. str.* species

The genus *Graphium* was described in 1837 (Corda 1837), with *G. penicillioides* as type species. After Saccaro (1886) expanded the genus concept to include synnematous species with dry conidia, the genus became a silo for all kinds of species producing synnemata and by 1935 more than 120 species had been added to the genus (Seifert & Okada 1993, www.indexfungorum.org). Goidànich (1935) restricted the genus concept to its original definition of species producing aseptate conidia in slimy droplets on pigmented synnemata. This concept included the synnematous anamorphs of many *Ophiostoma* spp. that were treated for many years before and after that as *Graphium* spp. (Hedgcock 1906, Schwarz 1922, Seifert & Okada 1993), adding to the confusion in the delineation of the genus. Okada *et al.* (1998, 2000) exposed the polyphyly of the genus based on DNA sequences, and assigned the 11 species for which they could obtain cultures to four different orders. They also designated an epitype for *G. penicillioides*, representing *Graphium s. str.* (Okada *et al*. 2000). In the *Ophiostomatales*, the 11 *Graphium* species related to *Ophiostoma* were transferred to *Pesotum* (Okada *et al.* 1998, 2000, Harrington *et al.* 2001), currently considered a synonym of *Ophiostoma* (De Beer & Wingfield 2012, De Beer *et al.* 2012). An additional ten species have been excluded from both the *Ophiostomatales* and *Microascales* (Okada *et al.* 2000, De Beer *et al.* 2012). The remaining *Graphium* spp. for which sequence data are available were shown to separate in two lineages in the *Microascales* (Okada *et al.* 1998, 2000, Gibb & Hausner 2003, Hulcr *et al.* 2007, Kolařík & Hulcr 2009, Cruywagen *et al*. 2010, Paciura *et al.* 2010). The two lineages within the *Microascales* were also evident in our analyses (**Figs 2, 3**). The first of these two lineages corresponded with the *G. putredinis* complex *sensu* Okada *et al.* (1998). In a more comprehensive study on this complex of opportunistic human pathogens, Lackner & De Hoog (2011) showed that *G. cuneiferum, G. lesnei*, and *G. tectonae,* are all synonyms of *Parascedosporium putredinis*, discussed above under the *Microascaceae*. They also suggested that *G. fructicola* should be treated in *Pseudallescheria*. The second lineage of *Graphium* spp. in the *Microascales* evident in our analyses (**Fig. 2**) contained *G. penicillioides* together with several other species (**Fig. 3**). This lineage was previously referred to as the *G. penicillioides* aggregate or complex (Seifert & Okada 1993, Okada *et al.* 1998, 2000).

Okada *et al.* (1998) emended the genus description of *Graphium* to include both the *G. penicillioides* and *G. putredinis* complexes after they excluded the non-Microascalean species from the genus. With the *G. putredinis* complex currently treated as *Parascedosporium* (Gilgado *et al*. 2007, Lackner & De Hoog 2011), the generic concept of *Graphium s. str.* again needed to be emended. Based on available SSU and ITS sequences, Cruywagen *et al*. (2010) included eight described and seven undescribed species together with *G. penicillioides* in *Graphium s. str*. All these species are known only by their anamorphs and were isolated from stained sapwood, wounds on trees, or from bark or ambrosia beetles (Mouton *et al*. 1994, Okada *et al.* 1998, 2000, Jacobs *et al.* 2003, Geldenhuis *et al.* 2004, Hulcr *et al*. 2007, Massoumi Alamouti *et al*. 2007, Kolařík & Hulcr 2009, Cruywagen *et al*. 2010, Paciura *et al*. 2010). De Beer *et al.* (2012) thus emended the description of *Graphium s.str.* based on *G. penicillioides* and the seven described species which forms a monophyletic lineage with it.

The multigene analyses by Zhang *et al.* (2006), Spatafora *et al*. (2006), and Schoch *et al.* (2009), confirm the separation of *Graphium s. str.* from *Microascus* and its allied genera, as was present in our phylogenetic analyses (**Figs 2, 3**). We are convinced that the phylogenetic distance between *Graphium* and the other families in the *Microascales* is sufficient to justify the description of a new family to accommodate the genus (**Box 1**). The Code (see Art.18.1, McNeill *et al.* 2006) dictates that a new family name is 'formed from the genitive singular of a name of an included genus,' in this case *Graphium*. This left us with no option but to use the derived name, *Graphiaceae*, to accommodate *Graphium* spp. This is unfortunate, since there are already several similar names: *Graphidaceae* (*Ostropales*), *Graphinellaceae* (= *Odontotremataceae*, *Ostropales*), *Graphiolaceae* (*Exobasidiales*) and *Graphostromataceae* (*Xylariales*) (Kirk *et al.* 2008).

The uncertain position of *Sphaeronaemella* in the *Microascales*

The genus *Sphaeronaemella* was first treated in the *Ophiostomataceae* by Müller & Von Arx (1973) based on superficial morphological similarities with *Ophiostoma* and *Ceratocystis*. The genus was subsequently reduced to synonymy with *Ceratocystis s. l.* by Upadhyay (1978, 1981), but the synonymy was disputed by Cannon & Hawksworth (1982), De Hoog & Scheffer (1984), and Hutchison & Reid (1988), based on the oblate ascospores with narrow germ slits, the gabarnaudia-like anamorphs, and the coprophilous nature of some *Sphaeronaemella* species. Benny & Kimbrough (1980) treated *Sphaeronaemella* as a distinct genus in the *Ophiostomataceae* and *Ophiostomatales* together with *Ophiostoma*, *Ceratocystis* and *Ceratocystiopsis*. Cannon & Hawksworth (1982) split *Sphaeronaemella*, retaining only *S. helvellae* in the genus and placing three species in *Viennotidia* (as '*Viennotidea*'). However, because *Viennotidia* was invalidly described by Negru & Verona (1966), Cannon & Hawksworth (1982) validated the genus, without recognizing that Rogerson (1970) had done so already, and they rejected the synonymy between *Viennotidia* and *Sphaeronaemella* suggested by Malloch (1974). Hutchison & Reid (1988) supported Malloch's synonymy, and this was finally confirmed with DNA sequence data by Hausner & Reid (2004). Spatafora & Blackwell (1994) verified the relationship between *Ceratocystis* and *Sphaeronaemella*, and their placement in the *Microascales*.

In his treatment of *Paecilomyces*, Samson (1974) described a new anamorph genus, *Gabarnaudia*, to accommodate *Paecilomyces betae*, the anamorphs of *S. fimicola* and *S. humicola*, and a new species, *Ga. tholispora*. Hausner & Reid (2004) showed that *Ga. betae* formed a monophyletic lineage with *S. fimicola* and *S. helvellae*, which was also present in our analyses (**Fig. 3**). Applying one fungus one name principles, *Gabarnaudia* is at present treated as synonym of *Sphaeronaemella* (De Beer *et al.* 2012).

In our analyses (**Figs 2, 3**), *Sphaeronaemella* also grouped within the *Microascales*. In the LSU analyses (**Fig. 2**) the genus grouped between the *Ceratocystidaceae* and the *Gondwanamycetaceae*. Based on SSU sequences, it grouped closer to the *Graphiaceae* (**Fig. 3**), although without statistical support. However, the ribosomal RNA operon of *Sphaeronaemella* has a unique, compact arrangement, which is reflected by reduced secondary structures when compared to those of *Ceratocystis*, *Cornuvesica* and *Gondwanamyces* (Hausner *et al.* 1993a, Hausner & Wang 2005). The LSU sequence of *S. fimicola* (U47839), for example, possesses six deletions which cause the sequence to have 198 gaps in the aligned data set when compared to *C. fimbriata*. This feature complicates the alignment and analyses of rDNA sequences of this genus with other groups, and prevents an accurate phylogenetic placement of *Sphaeronaemella* in the absence of data for other gene regions. We thus prefer to treat *Sphaeronaemella* for the present as of uncertain status in the *Microascales*.

GENERA OF DOUBTFUL AFFILIATION WITH THE *OPHIOSTOMATALES* AND *MICROASCALES*

The ever-changing concepts of orders, families and genera resulted in many unusual genera being included with the ophiostomatoid fungi in families and orders. Most of these were eventually shown to be unrelated and were thus excluded from the *Ophiostomatales* and *Microascales* (Table 1). However, the ordinal classification and generic status of eight genera, which have been suggested to be part of the *Ophiostomatales* and/or the *Microascales*, are uncertain at present and are discussed below.

Klasterskya and *Spumatoria*

Petrak (1940) described *Klasterskya* from dead pine and spruce needles, and suggested that it belongs in the *Ophiostomataceae* based on its long-necked perithecia and evanescent asci. Müller & Von Arx (1962) treated the genus in the *Sphaeriaceae*, but Minter (1983) redisposed *Klasterskya* in the *Ophiostomataceae*, based on the discharge of ‘ascospores in gummy masses’, and the presence of a hyalorhinocladiella-like conidiogenous cell arising from a septate ascospore. Valldosera & Guarro (1989) described another two species in the genus, but these were coprophiles. Malloch & Blackwell (1990) discussed several coprophilous fungi in their description of *Kathistes*, distinguished between the type species of *Klasterskya* and *Kathistes*, and questioned whether the two species of Valldosera & Guarro (1989) really belonged in *Klasterskya.* In our opinion the similarities between *Klasterskya* and *Kathistes* are much more evident than the suggested similarities with *Ophiostoma* or *Ceratocystis* spp.

The monotypic genus *Spumatoria* was described as part of a large study on coprophilous fungi by Massee & Salmon (1901). The fungus has apparently not been seen again, but was considered the closest relative of *Kathistes* by Malloch & Blackwell (1990), based on very similar morphology and coprophilous habit. In the same study these authors proposed the *Kathistaceae* to accommodate *Kathistes* in the *Ophiostomatales* (Malloch & Blackwell 1990). Based on the possible relatedness of *Spumatoria* with *Kathistes* as suggested by Malloch & Blackwell (1990), and the earlier suggestions that *Klasterskya* belonged in the *Ophiostomataceae* (Petrak 1940, Minter 1983), these two genera were treated in the *Ophiostomataceae* by Hawksworth *et al.* (1995) and Kirk *et al.* (2001, 2008). However, studies based on DNA sequence comparisons excluded *Kathistes* not only from the *Ophiostomatales* and *Microascales,* but from the ‘the main body of perithecial ascomycetes’ (Blackwell & Spatafora 1994, Blackwell & Jones 1997). We included a SSU sequence of *Kathistes calyculata* (AF313768) from the study of Blackwell *et al*. (2003) in our initial analyses, but the sequence proved to be inordinately divergent from the rest of our data, preventing us to include it in the final analyses. A BLAST search revealed that its closest relatives are species of *Hortaea* and *Teratosphaeria* in the *Dothideomycetes*. Based on the presence of septate ascospores and other similarities with *Kathistes* (Malloch & Blackwell 1990), and the great phylogenetic distance between the *Kathistaceae* (Dothideomycetes) and the *Ophiostomatales* and *Microascales* (Sordariomycetes) (Hibbett *et al*. 2007), we exclude both *Klasterskya* and *Spumatoria* from the latter two orders.

Rhynchophoma

The synonymy of *Rhynchophoma* with *Ceratocystis* (Hawksworth *et al.* 1983, 1995, Kirk *et al.* 2001) was based on the suggestion by Petrak (1953) that the type species, *R. crypta*, 'could be identical' to *Ceratostomella subpilosa*. Thus Petrak (1953) considered *Rhynchophoma* a synonym of *Ceratostomella*. Although the distinctions between *Ceratostomella* and *Ophiostoma* (Sydow & Sydow 1919), and *Ceratostomella* and *Ceratocystis* (Bakshi 1951), were made before Petrak's paper, his synonymy of *Rhynchophoma* and *Ceratostomella* somehow evolved into *Rhynchophoma* being listed as a synonym of *Ceratocystis* (Hawksworth *et al.* 1983). The synonymy of *Rhynchophoma* and *Ceratostomella* was upheld by Sutton (1977) and Verkley (2002). However, Réblová (2006) restricted *Ceratostomella* to species with pigmented ascospores in persistent asci (Von Arx 1952), while *Rhynchophoma* is characterised by septate ascospores (Karsten 1884). Réblová (2006) placed *Ceratostomella* species with septate spores in *Lentomitella*, and suggested that *C. subpilosa* should be transferred to this genus. If the synonymy between *C. subpilosa* and *R. crypta* can be confirmed, *Rhynchophoma* will take preference as the older name, with *Lentomitella* as synonym. Réblová (2006) confirmed the phylogenetic position of *Ceratostomella* and *Lentomitella* as outside both the *Ophiostomatales* and *Microascales* in the Sordariomycetidae (**Figs 2, 3**). We thus exclude *Rhynchophoma* from the *Ophiostomatales* and *Microascales* based on the characters that distinguish it from species in both orders.

Chaetonaemosphaera

Sutton (1977) suggested *Chaetonaemosphaera* might be a synonym of *Ceratocystis*. The genus was not mentioned in the *Ceratocystis* monograph by Upadhyay (1981), but the synonymy was acknowledged by Hawksworth *et al.* (1983, 1995) and Kirk *et al.* (2001, 2008). *Chaetonaemosphaera* was erected to accommodate *Naemosphaera vassiljevskii* (Kravtzev 1955, Byzova 1968). Illustrations of the long-necked ascomata, covered with ornamental hyphae, and the pigmented ascospores (Byzova 1968) certainly does not resemble any valid *Ceratocystis* spp. However, the depicted structures are strikingly similar to those in illustrations of several *Microascus* spp. treated by Barron *et al.* (1961), as well as *M. giganteus* (Malloch 1970). We thus reject the synonymy of *Chaetonaemosphaera* with *Ceratocystis* (Sutton 1977) and exclude it from the *Ophiostomatales* and *Ceratocystidaceae.* However, based on the similarities with *Microascus*, we suggest that the species should be considered in future treatments of the *Microascaceae*.

Mycorhynchella

The type species of the genus *Mycorhynchella* was suggested by Sutton (1977) to be 'an overmature *Ceratocystis'* in the Pilifera group of *Ceratocystis s. l.,* as defined by Olchowecki & Reid (1974). This group is treated as *Ophiostoma s. str.* (De Beer & Wingfield 2012). As a result of Sutton's (1977) suggestion, *Mycorhynchella* was treated as a synonym of *Ceratocystis* by Hawksworth *et al.* (1983, 1995) and Kirk *et al.* (2001, 2008). *Mycorhynchella* was initially described to accommodate three species with hyaline ascomata, producing cylindrico-fusoid (Petch 1943) or falcate (Sutton 1977) ascospores, sometimes septate (Von Höhnel 1918a, Petch 1943). The only ophiostomatoid species with septate ascospores is *Cornuvesica falcata*, with sheathed spores that are 15-28 µm long (Viljoen *et al.* 2000), while those of *M. exilis* are not sheathed and only 4 µm long (Sutton 1977). The description of *M. glomerata* resembles those of some of the *Ophiostoma* spp. with light-coloured perithecia, although the 'rose-coloured' ascomata is unique for this group (Petch 1943, Upadhyay 1981). However, the full description of *M. exilis* does not resemble any known species currently classified in the *Ophiostomatales* and *Ceratocystidaceae*, which makes a decision on the correct placement of the genus impossible at present. We thus treat *Mycorhynchella* as of uncertain status.

Canariomyces

The genus *Canariomyces* was described from *Phoenix canariensis* litter in the Canary Islands (Von Arx 1984), and subsequently treated in the *Microascaceae* (Von Arx *et al*. 1988, Eriksson & Hawksworth 1993, Lumbsch & Huhndorf 2007, Kirk *et al*. 2008). However, an unpublished LSU sequence of the ex-type isolate of *C. notabilis* (CBS 548.83), type species of *Canariomyces*, is identical to sequences of *Thielavia subthermophila* from the studies of Stchigel *et al.* (2002) and Badali *et al*. (2011). The latter is a valid species of *Thielavia*, a genus in the family *Chaetomiaceae* (*Sordariales*) (Stchigel *et al.* 2002). LSU sequences are not variable enough to confirm a species synonymy between *C. notabilis* and *T. subthermophila*, so the relationship between the two species needs to be explored further with sequences of more variable regions. However, the morphological description of *C. notabilis* fits within the genus *Thielavia* (Von Arx 1975). The morphological and sequence similarities suggest that *Canariomyces* should be treated as a synonym of *Thielavia*, so we exclude *Canariomyces* from the *Microascaceae*.

Lanspora

The genus *Lanspora* was described by Hyde & Jones (1986) for a marine fungus producing ascospores with polar appendages, typical for many species in the *Halosphaeriaceae*. Spatafora *et al.* (2006) included the type species, *L. coronata*, in their multigene phylogeny of the Pezizomycotina, where the species grouped in the Sordariomycetes, closest to *Ophiostoma piliferum*. However, in their analyses the Sordariomycetes was represented in total by only 46 taxa. Jones *et al.* (2009) treated *Lanspora* in the *Ophiostomatales* based on ‘preliminary molecular data’. In our analyses of the Sordariomycetes, which focused on the Sordariomycetidae and Hypocreomycetidae, these subclasses were represented by many more taxa than in the study of Spatafora *et al*. (2006). The results (**Figs 2, 3**) showed that *Lanspora* grouped well outside the *Ophiostomatales*. We thus exclude it from the order and consider it as of uncertain affiliation in the Sordariomycetidae.

Sporendocladia

The genus *Sporendocladia* was validated and distinguished from *Chalara*, by Nag Raj & Kendrick (1975). Wingfield *et al*. (1987) transferred five species of *Phialocephala* to *Sporendocladia*, and clarified the uncertainty about the type species for the genus, *S. fumosa* (Sutton 1975). In the only two phylogenetic studies to date considering the genus *Phialocephala*, sequence data for two *Sporendocladia* spp. have been provided, namely *S. bactrospora* and *S. foliicola*. The latter was placed in the *Helotiales* based on an ITS sequence (Grünig *et al*. 2002), while LSU and SSU sequences placed *S. bactrospora* in a lineage of its own in the *Microascales* (Jacobs *et al*. 2003). Apparently as a result of the latter placement, *Sporendocladia* is now listed among the genera of the *Microascales* (Réblová & Seifert 2007, Kirk *et al.* 2008, www.indexfungorum.org). However, since sequences for the type species, *S. fumosa,* are not available, the correct ordinal position of *Sporendocladia* remains uncertain.

NON-FUNGAL GENERA

Four of the ophiostomatoid genera have homonyms in other kingdoms. One of these genera belongs to the Viridiplantae (green plants), and the other four in the Metazoa (animals). The inclusion of these genera in this review might be viewed upon as merely anecdotal. However, in view of present discussions about a BioCode (McNeill 1997, Hawksworth 2011b), and the growing number of online species lists, these genera are worth mentioning to avoid confusion. Article 18 of the draft BioCode proposes that these homonyms will be acceptable because ‘they were published under different Special Codes prior to a future date yet to be determined.’ However, such homonyms established on or after this future date, will not be accepted (Greuter *et al.* 2011). The species in the genera below are thus listed in the nomenclator by De Beer *et al*. (2012, Table 1) so as to encourage mycologists to avoid the use of these names in future descriptions of new fungal taxa.

Linostoma Wallich and *Linostoma* Jankowski

The flowering plant genus *Linostoma* Wallich (Thymelaeaceae, Viridiplantae) was described in 1828 and at present includes two valid species (http://www.theplantlist.org). Thus, when Von Höhnel (1918b) described a new genus, *Linostoma* Höhn., to accommodate *Ceratostomella pilifera* (now *Ophiostoma piliferum*), the name was invalid. This was because it was a later homonym for the plant genus, and even though the fungi and plants belong to two kingdoms, the nomenclature of both is governed by the International Code of Nomenclature for Algae, Fungi, and Plants (ICN) (McNeill *et al.* 2006, Norvell 2011). Sydow & Sydow (1919) corrected the situation by describing a new genus, *Ophiostoma*, for *C. pilifera*, with *Linostoma* Höhn. as synonym. Not commonly known is the fact that the name *Linostoma* was again used for another new genus, this time for an aquatic protist (Ciliophora, Protozoa) by Jankowski in 1978 (Foissner & Berger 1996, Al-Rasheid 1999). However, the monotypic genus *Linostoma* Jankowski remains valid, and can be used in parallel to the plant genus, since the nomenclature of protists is independently governed the International Code of Zoological Nomenclature (ICZM).

Graphium Scopoli

Of the four non-fungal genus names in question, *Graphium* Scopoli, a genus of mostly tropical swallowtail butterflies (Lepidoptera, Papilionidae) that was described in 1777, might potentially cause the most confusion. The taxonomy of this genus is unresolved, and different sources provide highly variable numbers of species currently included in the genus. The Catalogue of Life (http://www.catalogueoflife.org/) at present lists 113 species in this genus, while more than 140 species have been described in the fungal genus *Graphium* Corda (discussed above under *Graphiaceae*), although not all of them are treated in the genus anymore. Since the taxonomy of the Arthropoda is also governed by the ICZM, both genera are valid.

Ophiostoma Rudolphi

The fungal genus *Ophiostoma* Syd. was erected in 1919 (Sydow & Sydow 1919). This was exactly a century after the genus *Ophiostoma* Rudolphi was described for five species of parasitic nematodes (Spirurida, Nematoda) occurring in the intestines of mammals and fish (Rudolphi 1809, 1819). An additional nine species was subsequently described in the genus (Table 1 in De Beer *et al.* 2012). The type species of *Ophiostoma* Rudolphi is currently treated in the older genus *Cystidicola*, with the result that *Ophiostoma* Rudolphi is now a synonym of the latter (Skriabin 1991). Some of the other *Ophiostoma* Rudolphi species are treated in *Rictularia* (Skriabin 1991), and the status of the remaining species is uncertain. The taxonomy of the Nematoda is governed by the ICZM, which means the status of *Ophiostoma* Syd. is not affected by the status of *Ophiostoma* Rudolphi.

Ceratocystis Jaekel

Eleven years after *Ceratocystis* Ellis & Halst. was described to accommodate the plant pathogen, *C. fimbriata* (Halsted 1890), Jaekel (1901) used the same genus name (*Ceratocystis* Jaekel) for the fossil of a small, extinct invertebrate (Echinodermata, Stylophora). He also described a new family, *Ceratocystidae* Jaekel, based on the genus name. Two more species were described by Ubaghs (1967, 1987), and a fourth as recent as 2010 by Rahman *et al*. (2010). The species names are listed by De Beer *et al.* (2012 in Table 1). This group of organisms are considered an important link in the early evolution of the echinoderms (Clausen & Smith 2005). The genus and family is valid because the taxonomy of these fossilized organisms is governed by the ICZM.

CONCLUSIONS

The purpose of the present study was to do undertake a retrospective analysis and consider the consequences of DNA sequencing on the taxonomy of the ophiostomatoid fungi at an ordinal level. We consolidated and re-assessed the current knowledge and all available sequence data, which enabled us to clarify and redefine the higher classification of these fungi. Although the ophiostomatoid fungi have now been clearly separated in two subclasses and orders of the Sordariomycetes, the major genera and species will still be considered together in future studies. This is not only as a result of their interwoven taxonomic history, but also their similar ecology.

The *Ophiostomatales*, as one of eight orders in the Sordariomycetidae, at present accommodates a single family with six valid genera. Based on these results, we have emended the descriptions of the order and family, both of which were outdated. The delineation of some genera remains to be clarified, preventing us from describing new families in the order at the present time.

The *Microascales* is one of six orders in the Hypocreomycetidae, and consists of five families. The formal description of two of these, the *Microascaceae* and *Halosphaeriaceae*, needs to be emended. The fifth family, the *Graphiaceae*, is newly described in the present study to accommodate the emended genus *Graphium*.

Many genera that have been treated in the *Ophiostomatales* or *Microascales* in the past, have been excluded from these orders. The status of eight of these remained uncertain. These genera were considered and five are excluded from these orders. For three genera we could not find sufficient evidence to arise at a satisfactory conclusion, and the position of these unfortunately remains uncertain.

Finally, four of the ophiostomatoid genera have homonyms in other Kingdoms. We considered these briefly and argue that species names in these genera should be avoided in future descriptions of fungal species in genera of the same names, since it will cause confusion.

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Table 1 Genera previously treated in the ophiostomatoid families and orders.

Genus	**Suggested Family and/or Order**	**Included by:**	**Excluded by:**
Ambrosiozyma	*Ophiostomataceae*	Von Arx 1974	Benny & Kimbrough 1980, Kurtzman & Robnett 1998
Botryoascus (=Saccharomycopsis)	*Ophiostomataceae*	Von Arx 1974	Benny & Kimbrough 1980, Kurtzman & Robnett 1998
Cephaloascus	*Ophiostomataceae*	Von Arx 1974	Benny & Kimbrough 1980, Kurtzman & Robnett 1998
Anekabeeja	*Microascaceae*	Udaiyan & Hosagoudar 1991, Eriksson & Hawksworth 1993	Korf 1995, Kirk *et al.* 2008
Canariomyces (?=Thielavia)	*Microascaceae*	Von Arx *et al.* 1988	this study, see text
Cephaloascus etc.	*Cephaloascaceae, Ophiostomatales*	Von Arx & Van der Walt 1987	Kurtzmann & Robnett 1998
Ceratostomella	*Ceratostomataceae*	Davidson 1935	Réblová 2006
Chadefaudia	*Ophiostomataceae*	Feldmann-Mazoyer 1957	Kohlmeyer 1972, Benny & Kimbrough 1980
Chadefaudiella	*Chadefaudiellaceae, Microascales*	Benny & Kimbrough 1980	Réblová *et al.* 2011
Chaetoceratostoma (=Scopinella)	*Ophiostomataceae*	Goidànich 1935, synonymy Hawksworth 1975	Zhang & Blackwell 2002
Chaetonaemosphaera (=Ceratocystis)	*Incertae sedis, Microascales*	Sutton 1977, Hawksworth *et al.* 1983	this study, see text, possibly in *Microascaceae*
Endomyces	*Endomycetaceae (=Ophiostomataceae)*	Redhead & Malloch 1977	Benny & Kimbrough 1980, Suh *et al*. 2001
Faurelina	*Pithoascaceae (=Microascaceae), Microascales*	Udagawa & Furuya 1973, Benny & Kimbrough 1980, Tang *et al*. 2007, synonymy Kirk *et al.* 2008	Réblová *et al.* 2011
Hormoascus (=Ambrosiozyma)	*Ophiostomataceae*	Von Arx 1974, synonymy Van der Walt & Von Arx 1985	Kurtzman & Robnett 1998
Kathistes	*Kathistaceae, Ophiostomatales*	Malloch & Blackwell 1990	Blackwell & Spatafora 1994
Klasterskya	*Ophiostomataceae*	Petrak 1940, Minter 1983	this study, see text
Lanspora	*Ophiostomatales*	Jones *et al.* 2009	this study, see text
Leuconeurospora	*Microascaceae*	Von Arx 1978	Suh & Blackwell 1999; Schoch *et al*. 2009
Microascus	*Ophiostomataceae*	Gäumann 1952	Barr 1990; Spatafora & Blackwell 1994
Mycorhynchella	*Incertae sedis, Microascales*	Sutton 1977; Hawksworth *et al*. 1983	this study, see text, placement uncertain
Ophiostomella (=Scopinella)	*Ophiostomataceae*	Goidànich 1935; synonymy Kirk *et al.* 2008	Zhang & Blackwell 2002
Petriella	*Ophiostomataceae*	Gäumann 1952	Barr 1990; Spatafora & Blackwell 1994
Phialocephala	*Ophiostomataceae*	Upadhyay 1981	Mouton *et al*. 1992; Jacobs *et al*. 2003
Pidoplitchkoviella	*Pithoascaceae, Microascaceae*	Eriksson 1984, Von Arx 1987, Hawksworth *et al.* 1995	Suh & Blackwell 1999
Pithoascus	*Pithoascaceae (=Microascaceae), Microascales*	Benny & Kimbrough 1980; synonymy Kirk *et al*. 2008	Barr 1990
Pseudeurotium etc.	*Pseudoeurotiaceae, Ophiostomatales*	Von Arx & Van der Walt 1987	Suh & Blackwell 1999
Pyxidiophora	*Pyxidiophoraceae, Ophiostomatales*	Von Arx & Van der Walt 1987	Blackwell & Spatafora 1994
Rhynchonectria	*Pyxidiophoraceae*	similar to *Pyxidiophora*, Malloch & Blackwell 1990	Malloch & Blackwell 1990 rejected the name
Rhynchophoma (=Ceratocystis)	*Incertae sedis, Microascales*	Hawksworth *et al*. 1983	this study, see text
Sporendocladia	*Microascales*	Réblová & Seifert 2007, Kirk *et al*. 2008	this study, see text, placement uncertain
Spumatoria	*Ophiostomataceae*	Hawksworth *et al.* 1995, Kirk *et al*. 2001	this study, see text
Subbaromyces	*Ophiostomataceae*	Cole *et al.* 1974, Hawksworth *et al.* 1995, Kirk *et al.* 2001	Benny & Kimbrough 1980, Blackwell & Jones 1997
Treleasia (=Pyxidiophora)	*Pyxidiophoraceae*	synonymy Lundqvist 1980	Malloch & Blackwell 1990, 1993

Box 1 A brief nomenclator of orders and families in which the ophiostomatoid fungi are classified.

Ophiostomatales Benny & Kimbr., Mycotaxon 12: 48. 1980. emend. Z.W. de Beer, Seifert & M.J. Wingf.
Type family: *Ophiostomataceae.*

Ascocarps globose, dark, carbonaceous, rarely light colored, ostiolate or nonostiolate, most often with elongate beak, ostiolar hyphae absent or present; asci evanescent; ascospores unicellular, sometimes with gelatinous sheath, reniform, allantoid, cylindrical, lunate, fusiform, falcate, hat-shaped or pillow-shaped; anamorphs variable, hyalorhinocladiella-, leptographium-, pesotum-, raffaelea-, and/or sporothrix-like.

Ophiostomataceae Nannf., Nova Acta Regiae Soc. Sci. Upsal. 8: 30. 1932. emend. Z.W. de Beer, Seifert & M.J. Wingf.
Type genus: *Ophiostoma.*
Other genera: *Ceratocystiopsis, Fragosphaeria, Leptographium s. l., Raffaelea, Graphilbum.*

Family description the same as for the order.

Microascales Luttr. *ex* Benny & Kimbr., Mycotaxon 12: 40. 1980. emend. Z.W. de Beer, Seifert & M.J. Wingf.
= *Halosphaeriales* Kohlm., in Hawksworth & Eriksson, Syst. Ascomyc. 5: 179. 1986.
Type family: *Microascaceae.*
Other families: *Halosphaeriaceae, Ceratocystidaceae, Gondwanamycetaceae, Graphiaceae,* possibly *Chadefaudiellaceae*.
Note: Order description needs to be emended once the *Microascaceae* and *Halosphaeriaceae* have been redefined.

Microascaceae Luttr. *ex* Malloch, Mycologia 62: 734. 1970.
= *Lophotrichaceae* Seth, Nov. Hedwigia 19: 592. 1971.
= *Pithoascaceae* Benny & Kimbrough, Mycotaxon 12: 45. 1980.
Type genus: *Microascus* (= *Pithoascus, = Fairmania, = Nephrospora, =Peristomium*).
Other genera: *Doratomyces* (= *Cephalotrichum, = Stysanus*), *?Enterocarpus, Kernia* (= *Magnusia*), *Lophotrichus, Parascedosporium, Petriella, Petriellopsis, Pseudallescheria (= Petriellidium)*, *Scedosporium, Scopulariopsis*, *Trichurus*, *Wardomyces*.
Note: Generic definitions need revision and the family description needs to be emended.

Halosphaeriaceae E. Müll. & Arx *ex* Kohlm. Can. J. Bot. 50: 1951. 1972.
Type genus: *Halosphaeria.*
Other genera: *Aniptodera, Antennospora, Ascosacculus, Ceriosporopsis, Corollospora, Halosarpheia, Monodictys, Oceanitis, Periconia, Remispora, Sagaaromyces, Sigmoidea*,*Varicosporina,* and more than 30 monotypic genera (Jones *et al.* 2009, Sakayaroj *et al.* 2011).
Note: Generic definitions need revision and the family description needs to be emended.

Ceratocystidaceae Locq. *ex* Réblová, W. Gams & Seifert, Stud. Mycol. 68: 188. 2011.
= *Ceratocystaceae* Locq., Rev. Mycol., Supplément, 1 Table. 1972. [*nom. inval*. Art. 36]
Type genus: *Ceratocystis.*
Other genera: *Ambrosiella, Cornuvesica*, *Thielaviopsis.*

Gondwanamycetaceae Réblová, W. Gams & Seifert, Stud. Mycol. 68: 188. 2011.
Type genus: *Knoxdaviesia* (= *Gondwanamyces*).
Other genus: *Custingophora.*

?Chadefaudiellaceae Faurel & Schotter *ex* Benny & Kimbr., Mycotaxon 12: 46. 1980.
= *Chadefaudiellaceae* Faurel & Schotter, Compt. Rend. Hebd. Séances Acad. Sci. 249: 151. 1959. [*nom. inval.* Art. 36]
Type genus: *Chadefaudiella*.
Note: The status of this family is uncertain. See discussion under *Microascales* in main body of text.

Graphiaceae Z.W. de Beer, Seifert & M.J. Wingf. ***fam. nov.***
Type genus: *Graphium* (= *Rhexographium*) (see emended genus description by De Beer *et al.* (2012).

Teleomorphs not known. Conidiomata macronematous, synnematous, determinate, with dematiaceous stipes. Conidia produced in a transparent, slimy droplet, darkening with age. Hyphae of stipe pigmented, simple septate. Conidiophores penicillately branched, with two or three levels of branching, metulae often present. Conidiogenous cells in whorls of two to six, conidiogenesis enteroblastic, with percurrent, annelidic proliferation. Conidia hyaline, aseptate, cylindrical to obovoid, sometimes curved with age, bases truncate, often with distinct basal frill. In rare cases a synanamorph with obovoid, pigmented conidia is formed.

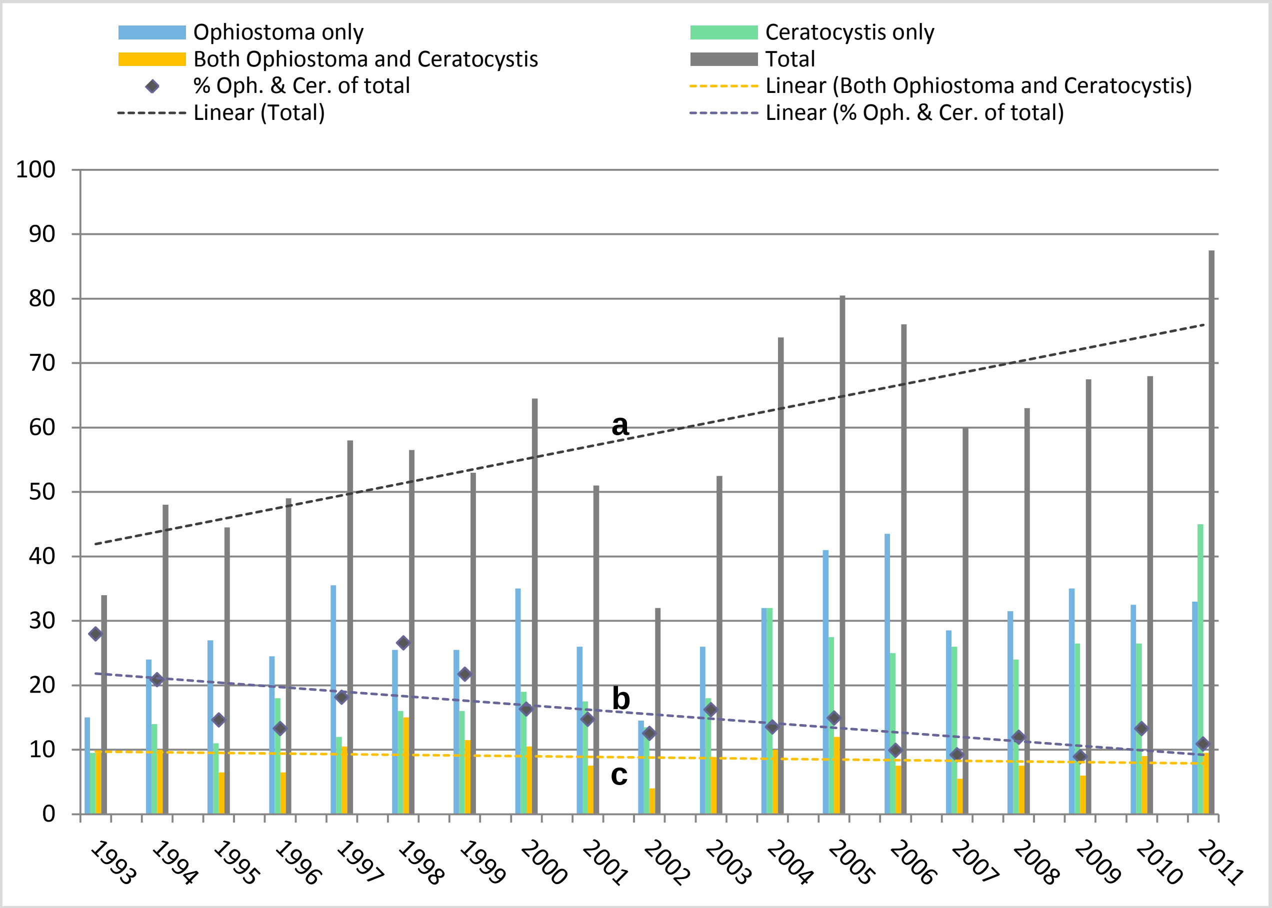
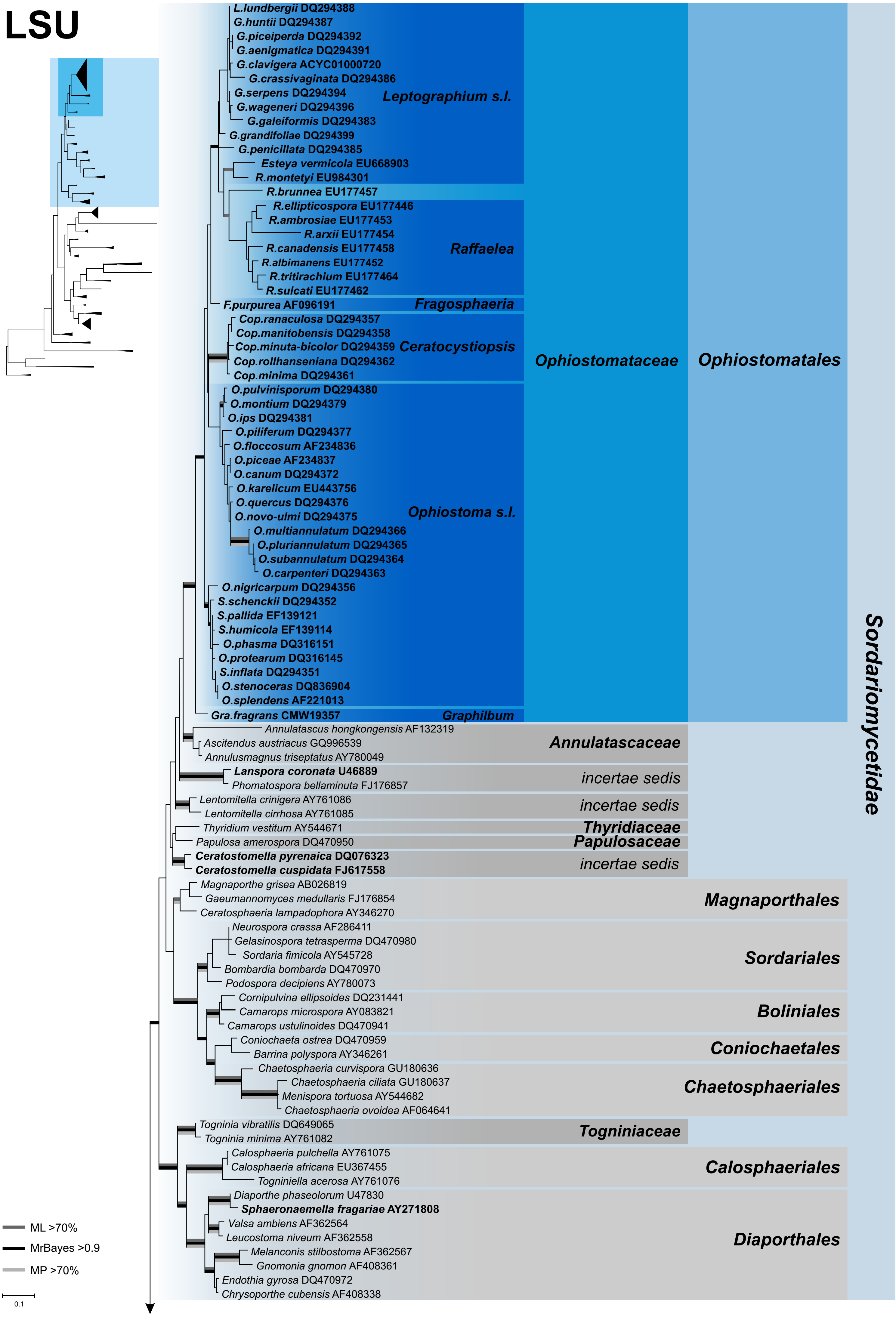


Fig. 1 Analyses of the number of publications annually since 1993, listing either *Ceratocystis* or *Ophiostoma,* or both genus names in the title, abstract and keywords. **a.** The linear trend of the total number of papers mentioning *Ceratocystis* and *Ophiostoma*. **b.** The linear trend based on the percentage of the number of papers mentioning both genus names, of the total number of papers published. **c.** The linear trend based on the actual number of papers mentioning both genera.

Fig. 2. A phylogenetic tree based on maximum likelihood (ML) analyses of the ribosomal LSU showing the higher classification of the ophiostomatoid fungi in the Sordariomycetes. The names of ophiostomatoid species, as well as species previously treated in the *Ophiostomatales* or *Microascales*, are printed in bold type. Support values for the different analyses are presented as bold lines at the nodes as indicated.


LSU
L.lundbergii DQ294388
G.huntii DQ294387
G.piceiperda DQ294392
G.aenigmatica DQ294391
G.clavigera ACYC01000720
G.crassivaginata DQ294386
G.serpens DQ294394
G.wageneri DQ294396
G.galeiformis DQ294383
G.grandifoliae DQ294399
G.penicillata DQ294385
Esteya vermicola EU668903
R.montetyi EU984301
Leptographium s.l.
R.brunnea EU177457
R.ellipticospora EU177446
R.ambrosiae EU177453
R.arxii EU177454
R.canadensis EU177458
R.albimanens EU177452
R.tritirachium EU177464
R.sulcati EU177462
Raffaelea
F.purpurea AF096191
Fragosphaeria
Cop.ranaculosa DQ294357
Cop.manitobensis DQ294358
Cop.minuta-bicolor DQ294359
Cop.rollhanseniana DQ294362
Cop.minima DQ294361
Ceratocystiopsis
O.pulvinisporum DQ294380
O.montium DQ294379
O.ips DQ294381
O.piliferum DQ294377
O.floccosum AF234836
O.piceae AF234837
O.canum DQ294372
O.karelicum EU443756
O.quercus DQ294376
O.novo-ulmi DQ294375
O.multiannulatum DQ294366
O.pluriannulatum DQ294365
O.subannulatum DQ294364
O.carpenteri DQ294363
Ophiostoma s.l.
O.nigricarpum DQ294356
S.schenckii DQ294352
S.pallida EF139121
S.humicola EF139114
O.phasma DQ316151
O.protearum DQ316145
S.inflata DQ294351
O.stenoceras DQ836904
O.splendens AF221013
Gra.fragrans CMW19357
Graphilbum
Ophiostomataceae
Ophiostomatales
Annulatascus hongkongensis AF132319
Ascitendus austriacus GQ996539
Annulusmagnus triseptatus AY780049
Annulatascaceae
Lanspora coronata U46889
Phomatospora bellaminuta FJ176857
incertae sedis
Lentomitella crinigera AY761086
Lentomitella cirrhosa AY761085
incertae sedis
Thyridium vestitum AY544671
Thyridiaceae
Papulosa amerospora DQ470950
Papulosaceae
Ceratostomella pyrenaica DQ076323
Ceratostomella cuspidata FJ617558
incertae sedis
Magnaporthe grisea AB026819
Gaeumannomyces medullaris FJ176854
Ceratosphaeria lampadophora AY346270
Magnaporthales
Neurospora crassa AF286411
Gelasinospora tetrasperma DQ470980
Sordaria fimicola AY545728
Bombardia bombarda DQ470970
Podospora decipiens AY780073
Sordariales
Cornipulvina ellipsoides DQ231441
Camarops microspora AY083821
Camarops ustulinoides DQ470941
Boliniales
Coniochaeta ostrea DQ470959
Barrina polyspora AY346261
Coniochaetales
Chaetosphaeria curvispora GU180636
Chaetosphaeria ciliata GU180637
Menispora tortuosa AY544682
Chaetosphaeria ovoidea AF064641
Chaetosphaeriales
Sordariomycetidae
Togninia vibratilis DQ649065
Togninia minima AY761082
Togniniaceae
Calosphaeria pulchella AY761075
Calosphaeria africana EU367455
Togniniella acerosa AY761076
Calosphaeriales
Diaporthe phaseolorum U47830
Sphaeronaemella fragariae AY271808
Valsa ambiens AF362564
Leucostoma niveum AF362558
Melanconis stilbostoma AF362567
Gnomonia gnomon AF408361
Endothia gyrosa DQ470972
Chrysoporthe cubensis AF408338
Diaporthales
ML >70%
MrBayes >0.9
MP >70%
0.1

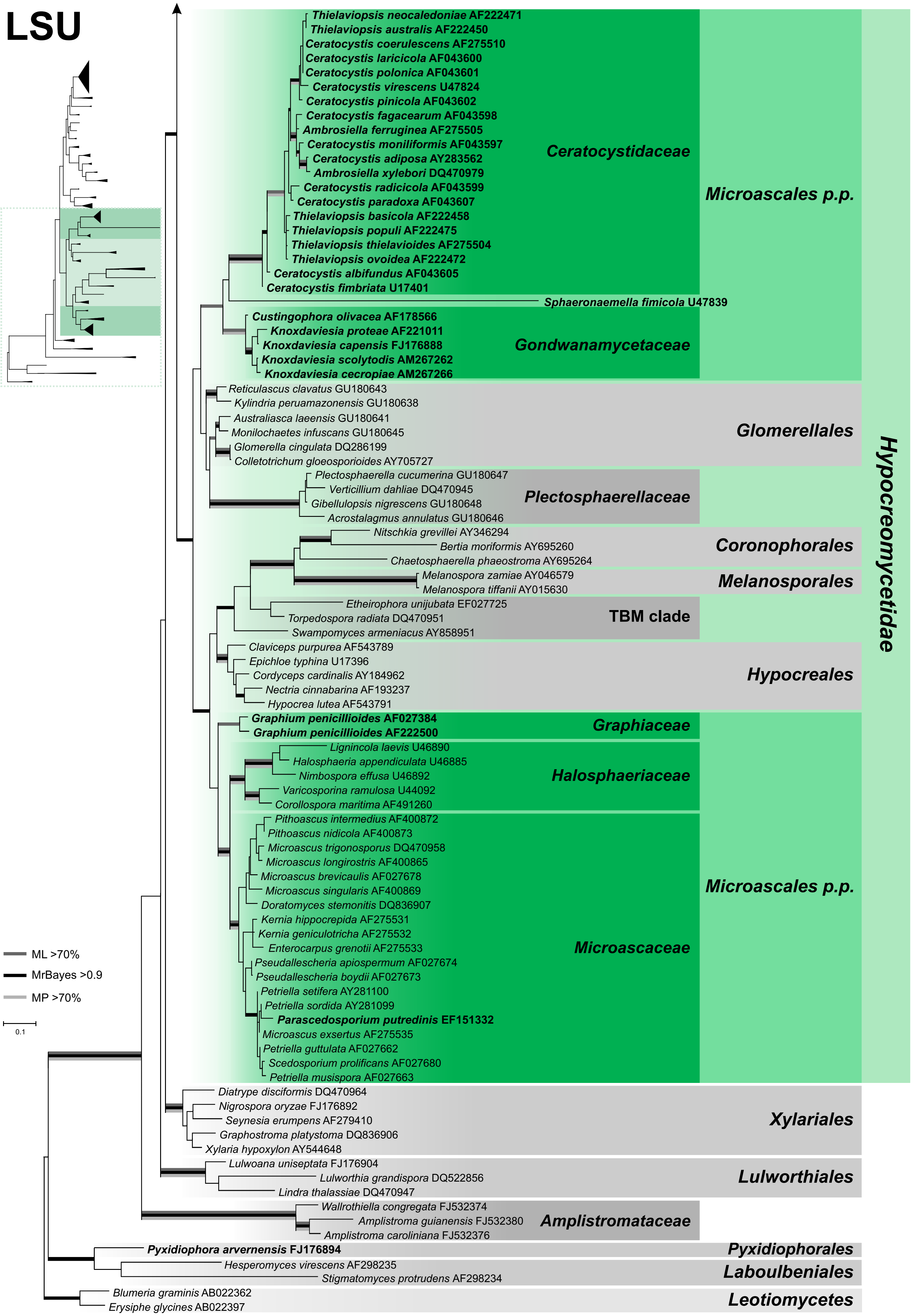
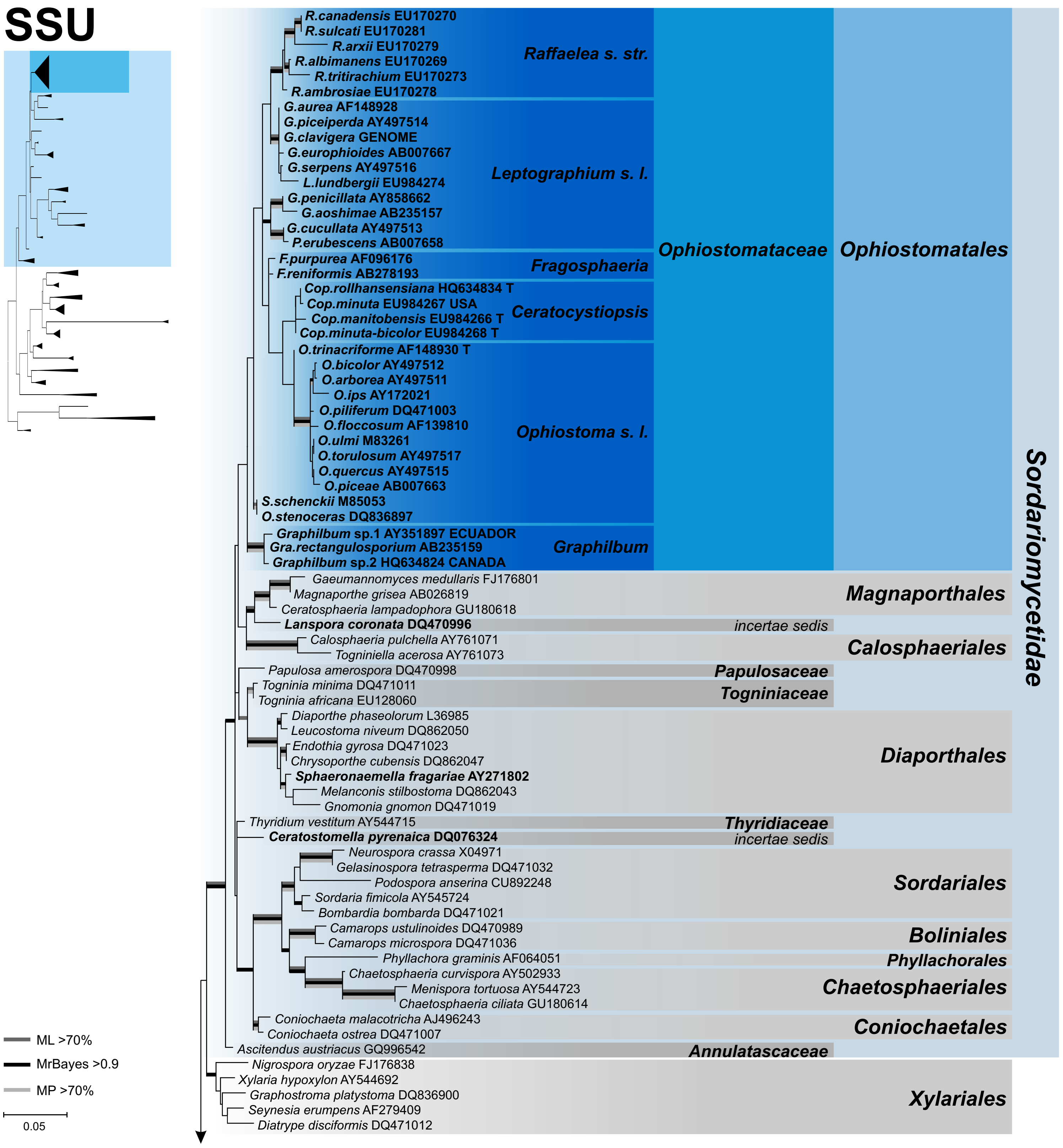

LSU
Thielaviopsis neocaledoniae AF222471
Thielaviopsis australis AF222450
Ceratocystis coerulescens AF275510
Ceratocystis laricicola AF043600
Ceratocystis polonica AF043601
Ceratocystis virescens U47824
Ceratocystis pinicola AF043602
Ceratocystis fagacearum AF043598
Ambrosiella ferruginea AF275505
Ceratocystis moniliformis AF043597
Ceratocystis adiposa AY283562
Ambrosiella xylebori DQ470979
Ceratocystis radicicola AF043599
Ceratocystis paradoxa AF043607
Thielaviopsis basicola AF222458
Thielaviopsis populi AF222475
Thielaviopsis thielavioides AF275504
Thielaviopsis ovoidea AF222472
Ceratocystis albifundus AF043605
Ceratocystis fimbriata U17401
Ceratocystidaceae
Microascales p.p.
Sphaeronaemella fimicola U47839
Custingophora olivacea AF178566
Knoxdaviesia proteae AF221011
Knoxdaviesia capensis FJ176888
Knoxdaviesia scolytodis AM267262
Knoxdaviesia cecropiae AM267266
Gondwanamycetaceae
Reticulascus clavatus GU180643
Kylindria peruamazonensis GU180638
Australiasca laeensis GU180641
Monilochaetes infuscans GU180645
Glomerella cingulata DQ286199
Colletotrichum gloeosporioides AY705727
Glomerellales
Plectosphaerella cucumerina GU180647
Verticillium dahliae DQ470945
Gibellulopsis nigrescens GU180648
Acrostalagmus annulatus GU180646
Plectosphaerellaceae
Nitschkia grevillei AY346294
Bertia moriformis AY695260
Chaetosphaerella phaeostroma AY695264
Coronophorales
Melanospora zamiae AY046579
Melanospora tiffanii AY015630
Melanosporales
Etheirophora unijubata EF027725
Torpedospora radiata DQ470951
Swampomyces armeniacus AY858951
TBM clade
Claviceps purpurea AF543789
Epichloe typhina U17396
Cordyceps cardinalis AY184962
Nectria cinnabarina AF193237
Hypocrea lutea AF543791
Hypocreales
Hypocreomycetidae
Graphium penicillioides AF027384
Graphium penicillioides AF222500
Graphiaceae
Lignincola laevis U46890
Halosphaeria appendiculata U46885
Nimbospora effusa U46892
Varicosporina ramulosa U44092
Corollospora maritima AF491260
Halosphaeriaceae
Pithoascus intermedius AF400872
Pithoascus nidicola AF400873
Microascus trigonosporus DQ470958
Microascus longirostris AF400865
Microascus brevicaulis AF027678
Microascus singularis AF400869
Doratomyces stemonitis DQ836907
Kernia hippocrepida AF275531
Kernia geniculotricha AF275532
Enterocarpus grenotii AF275533
Pseudallescheria apiospermum AF027674
Pseudallescheria boydii AF027673
Petriella setifera AY281100
Petriella sordida AY281099
Parascedosporium putredinis EF151332
Microascus exsertus AF275535
Petriella guttulata AF027662
Scedosporium prolificans AF027680
Petriella musispora AF027663
Microascaceae
Microascales p.p.
ML >70%
MrBayes >0.9
MP >70%
0.1
Diatrype disciformis DQ470964
Nigrospora oryzae FJ176892
Seynesia erumpens AF279410
Graphostroma platystoma DQ836906
Xylaria hypoxylon AY544648
Xylariales
Lulwoana uniseptata FJ176904
Lulworthia grandispora DQ522856
Lindra thalassiae DQ470947
Lulworthiales
Wallrothiella congregata FJ532374
Amplistroma guianensis FJ532380
Amplistroma caroliniana FJ532376
Amplistromataceae
Pyxidiophora arvernensis FJ176894
Pyxidiophorales
Hesperomyces virescens AF298235
Stigmatomyces protrudens AF298234
Laboulbeniales
Blumeria graminis AB022362
Erysiphe glycines AB022397
Leotiomycetes

Fig. 3. A phylogenetic tree based on maximum likelihood (ML) analyses of the ribosomal SSU showing the higher classification of the ophiostomatoid fungi in the Sordariomycetes. The names of ophiostomatoid species, as well as species previously treated in the *Ophiostomatales* or *Microascales*, are printed in bold type. Support values for the different analyses are presented as bold lines at the nodes as indicated.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R.canadensis EU170270
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R.tritirachium EU170273
R.ambrosiae EU170278
Raffaelea s. str.
G.aurea AF148928
G.piceiperda AY497514
G.clavigera GENOME
G.europhioides AB007667
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L.lundbergii EU984274
Leptographium s. l.
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G.aoshimae AB235157
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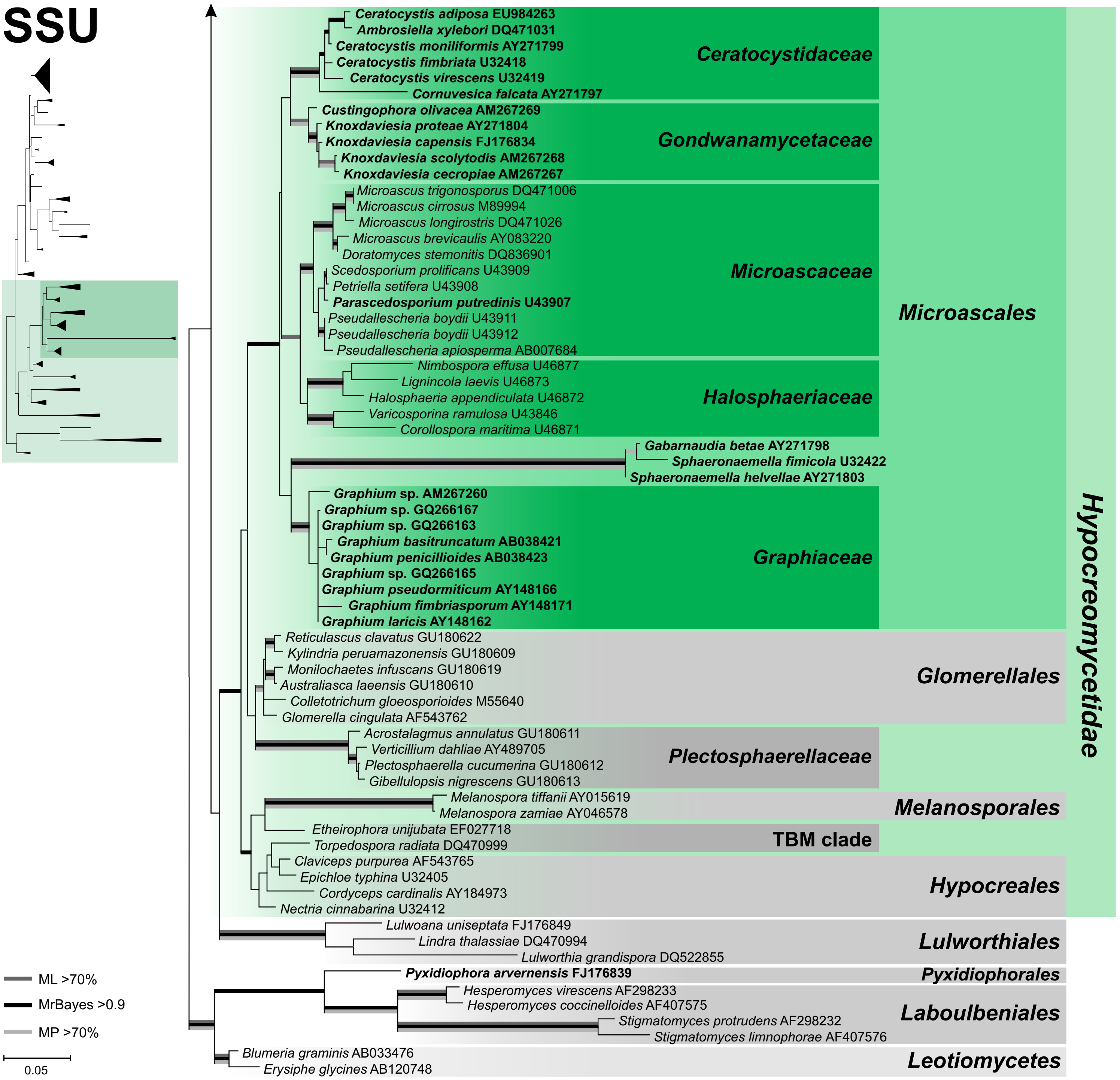
P.erubescens AB007658
F.purpurea AF096176
F.reniformis AB278193
Fragosphaeria
Cop.rollhansensiana HQ634834 T
Cop.minuta EU984267 USA
Cop.manitobensis EU984266 T
Cop.minuta-bicolor EU984268 T
Ceratocystiopsis
O.trinacriforme AF148930 T
O.bicolor AY497512
O.arborea AY497511
O.ips AY172021
O.piliferum DQ471003
O.floccosum AF139810
O.ulmi M83261
O.torulosum AY497517
O.quercus AY497515
O.piceae AB007663
Ophiostoma s. l.
S.schenckii M85053
O.stenoceras DQ836897
Graphilbum sp.1 AY351897 ECUADOR
Gra.rectangulosporium AB235159
Graphilbum sp.2 HQ634824 CANADA
Graphilbum
Ophiostomataceae
Ophiostomatales
Gaeumannomyces medullaris FJ176801
Magnaporthe grisea AB026819
Ceratosphaeria lampadophora GU180618
Magnaporthales
Lanspora coronata DQ470996
incertae sedis
Calosphaeria pulchella AY761071
Togniniella acerosa AY761073
Calosphaeriales
Papulosa amerospora DQ470998
Papulosaceae
Togninia minima DQ471011
Togninia africana EU128060
Togniniaceae
Diaporthe phaseolorum L36985
Leucostoma niveum DQ862050
Endothia gyrosa DQ471023
Chrysoporthe cubensis DQ862047
Sphaeronaemella fragariae AY271802
Melanconis stilbostoma DQ862043
Gnomonia gnomon DQ471019
Diaporthales
Thyridium vestitum AY544715
Thyridiaceae
Ceratostomella pyrenaica DQ076324
incertae sedis
Neurospora crassa X04971
Gelasinospora tetrasperma DQ471032
Podospora anserina CU892248
Sordaria fimicola AY545724
Bombardia bombarda DQ471021
Sordariales
Camarops ustulinoides DQ470989
Camarops microspora DQ471036
Boliniales
Phyllachora graminis AF064051
Phyllachorales
Chaetosphaeria curvispora AY502933
Menispora tortuosa AY544723
Chaetosphaeria ciliata GU180614
Chaetosphaeriales
Coniochaeta malacotricha AJ496243
Coniochaeta ostrea DQ471007
Coniochaetales
Ascitendus austriacus GQ996542
Annulatascaceae
Sordariomycetidae
Nigrospora oryzae FJ176838
Xylaria hypoxylon AY544692
Graphostroma platystoma DQ836900
Seynesia erumpens AF279409
Diatrype disciformis DQ471012
Xylariales
ML >70%
MrBayes >0.9
MP >70%
0.05



SSU
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Ambrosiella xylebori DQ471031
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Ceratocystis fimbriata U32418
Ceratocystis virescens U32419
Cornuvesica falcata AY271797
Ceratocystidaceae
Custingophora olivacea AM267269
Knoxdaviesia proteae AY271804
Knoxdaviesia capensis FJ176834
Knoxdaviesia scolytodis AM267268
Knoxdaviesia cecropiae AM267267
Gondwanamycetaceae
Microascus trigonosporus DQ471006
Microascus cirrosus M89994
Microascus longirostris DQ471026
Microascus brevicaulis AY083220
Doratomyces stemonitis DQ836901
Scedosporium prolificans U43909
Petriella setifera U43908
Parascedosporium putredinis U43907
Pseudallescheria boydii U43911
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Pseudallescheria apiosperma AB007684
Microascaceae
Microascales
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Halosphaeria appendiculata U46872
Varicosporina ramulosa U43846
Corollospora maritima U46871
Halosphaeriaceae
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Sphaeronaemella fimicola U32422
Sphaeronaemella helvellae AY271803
Graphium sp. AM267260
Graphium sp. GQ266167
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Graphium sp. GQ266165
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Graphium laricis AY148162
Graphiaceae
Hypocreomycetidae
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Kylindria peruamazonensis GU180609
Monilochaetes infuscans GU180619
Australiasca laeensis GU180610
Colletotrichum gloeosporioides M55640
Glomerella cingulata AF543762
Glomerellales
Acrostalagmus annulatus GU180611
Verticillium dahliae AY489705
Plectosphaerella cucumerina GU180612
Gibellulopsis nigrescens GU180613
Plectosphaerellaceae
Melanospora tiffanii AY015619
Melanospora zamiae AY046578
Melanosporales
Etheirophora unijubata EF027718
TBM clade
Torpedospora radiata DQ470999
Claviceps purpurea AF543765
Epichloe typhina U32405
Cordyceps cardinalis AY184973
Nectria cinnabarina U32412
Hypocreales
Lulwoana uniseptata FJ176849
Lindra thalassiae DQ470994
Lulworthia grandispora DQ522855
Lulworthiales
Pyxidiophora arvernensis FJ176839
Pyxidiophorales
Hesperomyces virescens AF298233
Hesperomyces coccinelloides AF407575
Stigmatomyces protrudens AF298232
Stigmatomyces limnophorae AF407576
Laboulbeniales
Blumeria graminis AB033476
Erysiphe glycines AB120748
Leotiomycetes
ML >70%
MrBayes >0.9
MP >70%
0.05

Chapter 2

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Emerging lineages in the *Ophiostomatales*

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Abstract

For many years, confusion between *Ceratocystis* and *Ophiostoma* obscured all major attempts to delineate genera and group species in the *Ophiostomatales*. The separation of *Ophiostoma* (*Ophiostomatales*) and *Ceratocystis* (*Microascales*) emerging from DNA-based phylogenetic inference resulted in the *Ophiostomatales* being represented by the single genus *Ophiostoma* at the end of the 20th century. The aim of this study was to review the impact that DNA sequencing and phylogenetic analyses has had on the taxonomy of the *Ophiostomatales* over the past two decades. As part of this study, all available sequence data for the *Ophiostomatales* were screened, carefully selecting representative ribosomal DNA sequences of 266 taxa residing in the order. We compiled these ribosomal large subunit and internal transcribed spacer region sequences in two data sets, containing 216 and 156 taxa respectively. Phylogenetic analyses of these data revealed six genera and 18 species complexes, as well as several lineages that could not be resolved. Five of the genera were well-defined: *Ophiostoma sensu stricto, Raffaelea s.str., Ceratocystiopsis*, *Fragosphaeria,* and *Graphilbum*, which was re-instated to accommodate species previously assigned to the *Pesotum fragrans* complex. However, several species complexes, including the *Sporothrix schenckii-O. stenoceras* complex, did not form part of *Ophiostoma s.str.* and were treated in *Ophiostoma sensu lato. Leptographium s.l.* was also not well-defined and included ten species complexes. Some of these complexes most likely represent distinct genera, but the currently available sequence data are not sufficient to define these. Our data also showed that *Raffaelea* is not monophyletic, and that the newly defined *R. lauricola* and *R. sulphurea* complexes group away from *Raffaelea s.str.*, respectively in *Ophiostoma s.l.* and *Leptographium s.l.* Our approach in defining genera was directed by the newly accepted one fungus one name principles incorporated in the ICN at Melbourne in 2011, and we discuss the impact that these changes will have on the taxonomy of the *Ophiostomatales* in the near future. We also make recommendations for dealing with taxa in the less well-defined lineages in the interim, and until a more robust multigene phylogeny becomes available for the *Ophiostomatales*.

A BRIEF HISTORY OF THE GENUS *OPHIOSTOMA*

The genus *Ophiostoma* typifies the order *Ophiostomatales sensu* De Beer *et al.* (2012a). The type species of *Ophiostoma*, *O. piliferum,* was described as *Sphaeria pilifera* in 1823 from stained conifer wood in Sweden (Fries 1823). At the time, *Sphaeria* included most fungi with either dark perithecia or pycnidia (Wakefield 1940). Fries listed 550 species under *Sphaeria*, which he classified based on the appearance of perithecia *in situ*. As increasing numbers of species were described towards the end of the 19th century, generic boundaries were more narrowly defined by taxonomists such as Saccardo and Winter (Bisby & Mason 1940). This resulted in *S. pilifera* first being transferred to *Ceratostoma* (Fuckel 1869), and then to *Ceratostomella* (Winter 1887). In 1906, Hedgcock retained the name *Ceratostomella pilifera* for the prevalent cause of sapstain in his study of wood-staining fungi in the United States. He also transferred another species, *Cs. echinella*, to *Ceratostomella* and described six new species in the genus. Münch (1907) considered the original species definition of *Cs. pilifera* inordinately broad, and described four new *Ceratostomella* species, three of which he treated as the `Pilifera group`. Von Höhnel (1918) transferred *Cs. pilifera* to a new genus, *Linostoma,* because he restricted *Ceratostomella* to species forming persistent asci, while the asci of *Cs. pilifera* were dehiscent. However, *Linostoma* was a later homonym for a genus of flowering plants (see De Beer *et al.* 2012a), and consequently Sydow & Sydow (1919) established the new genus, *Ophiostoma* for *Cs. pilifera,* the seven other *Ceratostomella* species treated by Hedgcock (1906), and the four species described by Münch (1907). Melin & Nannfeldt (1934) followed this approach by adding 11 species to *Ophiostoma,* including *Ceratocystis fimbriata*, the type species of *Ceratocystis*.

While *Ophiostoma* became widely recognised in Europe (Goidànich 1935, Siemaszko 1939, Bisby & Mason 1940, Mathiesen 1950, Rennerfelt 1950), authors on the other side of the Atlantic (Leach 1934, Rumbold 1936, 1941, Davidson 1935, 1942, Taylor-Vinje 1940, Shafer & Liming 1950) continued to treat the ophiostomatoid species in *Ceratostomella*. Bakshi (1950, 1951) treated *O. piceae*, *C. coerulescens* and four new species in *Ceratocystis,* arguing that *Ceratocystis* should have priority because the name was older than *Ophiostoma*. Moreau (1952) followed by transferring 31 species to *Ceratocystis*. Apparently unaware of the work of Bakshi (1951) and Moreau (1952), von Arx (1952) declared *Rostrella*, *Endoconidiophora*, *Linostoma*, *Grosmannia* and *Ceratostomella auct. non* Sacc., synonyms of *Ophiostoma*, and transferred 13 species of *Ceratostomella*, *Grosmannia* and *Endoconidiophora* to *Ophiostoma*. Von Arx & Müller (1954) responded to the works of Bakshi (1951) and Moreau (1952), arguing for the conservation of *Ophiostoma* against *Ceratocystis* to avoid unnecessary name changes for important plant pathogens. They transferred five additional species to *Ophiostoma* (von Arx & Müller 1954). Both von Arx's papers were published in German, and it is probably for this reason that Bakshi's classification, published in English, became widely accepted. The transfer of species from the other genera, including *Ophiostoma*, to *Ceratocystis,* was completed by Hunt (1956). For the next 30 years, all major publications dealing with this group of fungi (Davidson 1958, 1966, 1971, Mathiesen-Käärik 1960, Griffin 1968, Olchowecki & Reid 1974, Upadhyay 1978, 1981) treated *Ophiostoma sensu stricto* species in *Ceratocystis*.

All the treatments of *Ophiostoma* and *Ceratocystis* prior to 1967 considered only morphological characters. During the 1960's, however, biochemical characters emerged as an increasingly important aid to morphology in delineating taxa (Bartnicki-Garcia 1968). When cellulose was discovered in the hyphal walls of *O. ulmi* (as *C. ulmi*), it was considered an exception, because that polysaccharide had never before been found in any Ascomycete (Rosinski & Campana 1964). Soon cellulose was also detected in cell walls of other *Ceratocystis* spp. with 'exoconidial' anamorphs (thus *Ophiostoma* spp.), while species with 'endoconidial' anamorphs did not contain cellulose (Rosinksi 1965, Smith *et al.* 1967, Jewell 1974). Acknowledging these biochemical differences, De Hoog (1974) separated *Ceratocystis s.l.* into two distinct genera based on morphology of these anamorphs. *Ceratocystis s.str.* accommodated species with endoconidial anamorphs classified in *Chalara*, *Chalaropsis*, and *Thielaviopsis*, while species with exoconidial anamorphs classified in *Sporothrix*, *Verticicladiella*, *Leptographium*, and *Graphium*, were placed in *Ophiostoma* (De Hoog 1974, Weijman & De Hoog 1975). Confirming the conclusions based on cellulose content, Harrington (1981) showed that growth of *Ceratocystis s.str.* species was inhibited by cycloheximide, an antibiotic that disrupts protein synthesis, while growth of *Ophiostoma* species was generally unaffected. Although the separation of *Ophiostoma* from *Ceratocystis* gained support (Samuels & Müller 1978, De Hoog & Scheffer 1984, Solheim 1986, Harrington 1987, De Rulamort 1990), some authors still argued in favour of, and applied the concept of *Ceratocystis senso lato*, until the early 1990’s (Upadhyay 1981, 1993, Kowalski & Butin 1989). The term ‘ophiostomatoid fungi’ was coined to collectively refer to *Ophiostoma* and *Ceratocystis* species that commonly co-occur in niches associated with insects (Wingfield *et al.* 1993).

The first studies applying phylogenetic analyses of DNA sequence data to these fungi, finally confirmed the separation of the two genera and the placement of *Ophiostoma* in the *Ophiostomatales* and *Ceratocystis* in the *Microascales* (Hausner *et al.* 1993c, Spatafora & Blackwell 1994). The subsequent synonymy of *Ceratocystiopsis* with *Ophiostoma* (Wingfield 1993, Hausner *et al.* 1993a), left the *Ophiostomatales* by the late 1990’s represented by the single teleomorph genus *Ophiostoma*.

The newly defined *Ophiostoma* included species with a diverse array of anamorph types (**Fig. 1**), varying from synnematous pesotum-like anamorphs, to mononematous leptographium- and mycelial sporothrix-, hyalorhinocladiella-, and raffaelea-like anamorphs (Berbee & Taylor 1992, Okada *et al.* 1998, Hausner *et al.* 2000, Harrington *et al.* 2001, Jacobs *et al.* 2001b, Rollins *et al.* 2001). Ascomata varied from perithecia with hyaline to black bases with extremely long necks (e.g. *O. pluriannulatum*), to those with short necks (e.g. *O. minutum*) or cleistothecia with no necks (e.g. *O. aureum*) (**Fig. 2**). Ascospores were either sheathed or not, and included several shapes (**Fig. 3**). Over the years, there were many attempts to group species based on these morphological characters, with different authors emphasizing different characters. The first such classification was by Melin & Nannfeldt (1934), using perithecial morphology to define sections and anamorph morphology for subgroups. Hunt (1956) and Mathiesen-Käärik (1960) based their sections in the genus only on anamorph morphology, while Griffin (1968), Olchowecki & Reid (1974) and Upadhyay (1981) based their groups and sections on ascospore morphology. Because of similarities between *Ophiostoma* and *Ceratocystis* in many of these morphological features, all the attempts to group species based on these characters were confounded by the inclusion of *Ceratocystis* species.

THE IMPACT OF DNA SEQUENCING AND PHYLOGENETICS

With *Ceratocystis* ‘out of the way’ at the dawn of the new millennium, a new wave of taxonomic studies focusing on *Ophiostoma* and employing DNA sequences and phylogenetic analyses, began to emerge. These studies can be categorized broadly as follows, although many papers might fit in more than one category:

1. Definition of species complexes based on phylogeny and morphology (e.g. Harrington *et al.* 2001, De Beer *et al.* 2003a, Jacobs & Kirisits 2003, Kim *et al.* 2003, Lim *et al.* 2004, Gorton *et al.* 2004, Grobbelaar *et al.* 2009, Plattner *et al.* 2009, Linnakoski *et al.* 2010, 2012, Madrid *et al.* 2010, Zanzot *et al.* 2010, Duong *et al.* 2012).

2. Resolution of phylogenetic relatedness and species boundaries for single species, previously described (e.g. Schroeder *et al.* 2001, Hausner & Reid 2003, Zhou *et al.* 2004c, Jacobs *et al.* 2005, Marimon *et al.* 2008, Massoumi Alamouti *et al.* 2011).
3. Descriptions of new species (e.g. Uzunovic *et al.* 2000, Kim *et al.* 2004, Aghayeva *et al.* 2004, 2005, Villarreal *et al.* 2005, Jacobs *et al.* 2006, 2010, Ohtaka *et al.* 2006, Carlier *et al.* 2006, Greif *et al.* 2006, Marimon *et al.* 2007, Lu *et al.* 2008, Zhou *et al.* 2008, Roets *et al.* 2008, 2010, Kamgan *et al.* 2008a, 2010, 2011, 2012, Grobbelaar *et al.* 2010, Paciura *et al.* 2010a).
4. Determination of anamorph-teleomorph connections (e.g. De Beer *et al.* 2003, Kim *et al.* 2005c, Masuya *et al.* 2005, Yamaoka *et al.* 2008).
5. Identification of bark and ambrosia beetle associates (e.g. Jacobs *et al.* 2003, Zhou *et al.* 2004a, b, 2006, Hausner *et al.* 2005, Lim *et al.* 2005b, Massoumi Alamouti *et al.* 2006, 2007, Hulcr *et al.* 2007, Romón *et al.* 2007, Linnakoski *et al.* 2008, 2009, 2012, Lu *et al.* 2009a, b, Kim *et al.* 2009, 2011, Kolařík & Hulcr 2009, Jankowiak & Kolařík 2010a, Roe *et al.* 2010, Paciura *et al.* 2010b, Endoh *et al.* 2011, Six *et al.* 2011).
6. Identification of ophiostomatoid fungi collected during surveys from niches other than bark beetles, e.g. stained wood (Uzunovic *et al*. 1999; Kim *et al.* 2005a, b, Lim *et al.* 2005a, Thwaites *et al.* 2005), wounds on living trees (Geldenhuis *et al.* 2004, Kamgan *et al.* 2008b), airborne fungi in forests (Vasiliauskas *et al.* 2005), wood poles (De Meyer *et al.* 2008), *Protea* infructescenses (Roets *et al.* 2006, 2008, 2010), decaying grass (Shrestha *et al.* 2011), gardens of fungus-growing ants (Rodrigues *et al.* 2011), and human sporotrichosis (Galhardo *et al.* 2008, Oliveira *et al.* 2011, Romeo *et al.* 2011).
7. Reports of known species from new hosts or geographic locations (Bommer *et al.* 2009, Smith *et al.* 2009a, b, Grobbelaar *et al.* 2010, Jankowiak & Kolařík 2010b, Eskalen & McDonald 2011).
8. Metagenomic studies, where surveys and species identifications were made solely based on DNA samples, e.g. from roots (Menkis *et al.* 2006, Khidir *et al.* 2010), and decaying wood (Lindner *et al.* 2011).

In the majority of studies where phylogenetic analyses were undertaken, the species in question was treated in the context of a group of morphologically similar species, in some cases referred to as a species complex. Where DNA sequence data were unavailable for reference species, strains were obtained from international collections and sequences determined. Most of the earlier studies included only ribosomal DNA data, but it was soon realised that introns of protein-coding genes were very valuable for distinguishing closely related species, and multigene studies became the norm within the first few years of the new millenium. In many studies, an rDNA tree was included to show the position of the relevant species or complex in the genus, and these trees included between 11 (Schroeder *et al.* 2001) and 44 (Roets *et al.* 2006) taxa. Trees based on protein-coding genes were often included to distinguish between smaller subsets of species.

Only a few studies attempted to resolve groups at a generic level within the *Ophiostomatales*, and those that did, usually dealt with a very specific morphological group. The study of Hausner *et al.* (2000) assessed the phylogenetic positioning of eight *Leptographium* spp. and one *Pesotum* sp. among 27 *Ophiostoma* spp. using ribosomal small subunit (SSU) and large subunit (LSU) data, concluding that the separation between *Leptographium* and *Pesotum* is artificial. Shortly afterwards, Jacobs *et al.* (2001b) showed that internal transcribed spacer 2 (ITS2) and LSU sequences did not support morphological groups among 44 *Leptographium* spp., some with known teleomorphs. However, Jacobs *et al.* (2001b) did not include any *Ophiostoma* spp. with other anamorph morphologies in their analyses. In the same year, Rollins *et al.* (2001) showed that eight *Ambrosiella* (now *Raffaelea*) spp. grouped among six *Ophiostoma* spp. based on SSU. Although indicative of trends and morphological heterogeneity within the larger *Ophiostoma*, none of these studies attempted to define specific subgroups within the genus based on phylogenetic lineages.

The first study to address generic concepts in the *Ophiostomatales* based on multigene phylogenies applying protein-coding (β-tubulin exon) sequences in combination with those of the LSU, was published in 2006 (Zipfel *et al.* 2006). The resulting phylogenies that included 50 *Ophiostoma* spp, revealed two phylogenetic lineages distinct from *Ophiostoma* and supported by morphological features. These lineages were given generic status and two previously recognised genera were reinstated and redefined to accommodate species from these lineages. The first was *Grosmannia* (Goidànich 1936), which was defined apart from phylogeny, primarily by its *Leptographium* anamorphs and sheathed ascospores (Zipfel *et al.* 2006). Species in the second lineage were assigned to *Ceratocystiopsis,* initially described in 1975 (Upadhyay & Kendrick 1975) and typified by *Cop. minuta,* which are characterised by falcate ascospores and *Hyalorhinocladiella* anamorphs. *Ophiostoma* formed a monophyletic lineage and was also redefined, although it was recognized that it contained several distinct lineages (Zipfel *et al.* 2006). The reinstated genera gained wide support in the subsequent taxonomic literature (Roets *et al.* 2006, Romón *et al.* 2007, Six & Bentz 2007, Linnakoski *et al.* 2008, 2012, Yamaoka *et al.* 2008, Lu *et al.* 2009a, Massoumi Alamouti *et al.* 2009, Plattner *et al.* 2009, Jankowiak & Kolařík 2010a, Kirisits 2010, Matsuda *et al.* 2010, Reid & Hausner 2010, Roe *et al.* 2010, Kim *et al.* 2011). Some of these studies based their phylogenies on the phylograms of Zipfel *et al.* (2006), presenting expanded data sets that included 63 (Paciura *et al.* 2010a, Six *et al.* 2011), 65 (Linnakoski *et al.* 2010), 73 (Linnakoski *et al.* 2012) and 74 taxa (Duong *et al.* 2012), but none formally introduced new taxa above the species level.

CURRENT FORCES DIRECTING THE TAXONOMY OF THE *OPHIOSTOMATALES*

Twenty years have passed since the first DNA sequences for *Ophiostoma* were produced (Berbee & Taylor 1992). Apart from advances in DNA sequencing technology, other forces came into play that are having an immence impact on fungal systematics on the wider front, and thus also on the taxonomy of the *Ophiostomatales*.

The first of these was the Fungal Tree of Life (AFTOL) project (www.aftol.org), which endeavored to reconstruct the phylogeny of the Fungal Kingdom based on multiple gene regions including all major lineages of fungi (Lutzoni *et al.* 2004, Bruns 2006). The resulting phylogenies provided an accurate placement reflecting the evolutionary position of the *Ophiostomatales* in the fungal kingdom (Spatafora *et al.* 2006, Hibbett *et al.* 2007, Schoch *et al.* 2009). This ended a century of speculation and confusion regarding the higher level classification of *Ophiostoma* and allied genera based on a variety of human-selected criteria (Lindau 1897, Nannfeldt 1932, Luttrell 1951, Ainsworth 1963, 1971, Müller & Von Arx 1973, Benny & Kimbrough 1980, Barr 1990). The AFTOL classification provided a backbone for all treatments of fungi at a higher order level, including the *Ophiostomatales* (De Beer *et al.* 2012a), and will do so for years to come.

The second force that is having a substantial impact on fungal taxonomy is the accessibility of online databases that are part of the daily operational tools of fungal taxonomists. These include IndexFungorum (www.indexfungorum.org/), a nomenclatoral database listing the correct names and authorities of all fungal taxa; MycoBank (www.MycoBank.org), which lists valid fungal species with their associated descriptions, illustrations and references (Crous *et al.* 2004); Cyberliber (www.cybertruffle.org.uk/cyberliber/), an electronic library providing free access to many older mycological publications; and NCBI GenBank (www.ncbi.nlm.nih.gov/), providing access not only to almost all published DNA sequences, but also links to relevant publications. These resources enhance the accuracy of taxonomic publications, accelerating the rate at which they appear, and also assist in aligning the taxonomic literature following a more uniform format. However, an underlying risk is that errors in these databases can be perpetuated in the literature. This implies that mycologists must use data from these sources with care, and specialists should engage with the managers of the databases to correct errors when these are detected. These databases were used extensively in the present study, and also in those by De Beer *et al.* (2012a, b).

The third relatively new, yet hugely important driver influencing fungal taxonomy lies in the application of metagenomics to species discovery and identification. Although only a few such studies have thus far revealed ophiostomatoid species (Menkis *et al.* 2006, Khidir *et al.* 2010, Lindner *et al.* 2011), these technologies provide the power to explore new and known niches for fungal diversity, including ophiostomatoid species, much more thoroughly than ever before. All indications are that the diversity of fungal species is much greater than previously anticipated (Hawskworth 2001, Blackwell 2011), and suggestions are emerging on to how to accommodate novel taxa in the formal classification system of fungi known only from environmental DNA specimens (Hibbett *et al.* 2011, Taylor 2011).

Another factor that is beginning to make an impact on fungal systematics at various levels is whole genome sequencing (Robbertse *et al.* 2006, McLaughlin *et al.* 2009, Wang *et al.* 2009). The complete genomes of several ophiostomatalean fungi are becoming available (Bernier *et al.* 2004, DiGuistini *et al.* 2007, Hintz *et al.* 2011), and they have already been employed in the development of new genetic markers used in taxonomic studies (Tsui *et al.* 2009, Khadempour *et al.* 2010, Roe *et al.* 2010, Massoumi Alamouti *et al.* 2011, Duong *et al.* 2012). Furthermore, the 1000 Fungal Genomes Project (1000.fungalgenomes.org/), will undoubtedly result in many new developments and tools that will be appllied in fungal taxononomic studies.

The single largest catalyst for change in the taxonomy of fungi in the immediate future is the adoption of the one fungus: one name principle by the 2011 IBC (International Botanical Congress) in Melbourne (Hawksworth 2011, Hawksworth *et al.* 2011, Norvell 2011). The new version of the International Code for the Nomenclature of Algae, Fungi and Plants (ICN) will not allow the use of separate names for anamorphs of fungi with a pleomorphic life cycle after 1 January 2013 (Hawksworth 2011, Norvell 2011). Interestingly, the *Ophiostomatales* have played an important role in the initiation of the whole movement towards single name nomenclature. This occurred when Berbee & Taylor (1992) showed that it was possible to place an anamorphic fungus, *Sporothrix schenckii*, in a teleomorph genus, *Ophiostoma*, based on DNA sequences. One of the implications of the changes to the ICN is that older generic names have priority over newer names, irrespective of the morph they represent. The only exceptions will be if the newer names are conserved for some reason(s) against the older names. If not applied responsibly, these changes in the Code might result in many name changes and much confusion in the *Ophiostomatales*, as has been pointed out by Wingfield *et al.* (2012).

Subsequent to the Berbee & Taylor (1992) study, DNA sequence data have become available for 266 out of the 295 species currently considered as distinct in the *Ophiostomatales* (De Beer *et al.* 2012b). Yet the largest phylogeny to date included only 74 of these species (Duong *et al.* 2012). Considering the current developments in fungal taxonomy described above, and the presently available data for the *Ophiostomatales*, the time is ripe for an extensive analysis including data of very large numbers of species.

All previous analyses had as a starting point preconceived notions based on morphological traits that strongly impacted the selection of taxa. In contrast, the aim of the present study was to allow the DNA sequence data to determine the outcome. The resulting phylogenies should at the same time serve as a review of current knowledge, revealing evolutionary and ecological patterns. They should also provide a scaffold to direct future research and especially to guide decisions relating to the implementation of the one fungus one name principles.

PHYLOGENETIC ANALYSES

The major obstacle to a comprehensive phylogenetic overview of the *Ophiostomatales* is that past studies used different gene regions. Thus, no single analysis using one gene region could include the maximum number of species. The two regions for which the most data were available from GenBank were chosen here, namely the ribosomal LSU, and the internal transcribed spacer regions (ITS1, 5.8.S, ITS2). We evaluated β-tubulin and translation elongation factor 1α (EF-1α) regions, and although the results for the latter two gene regions are not presented here, the presence and absence of introns in these markers is mentioned because there is a strong correlation between lineages based on rDNA and intron arrangements in these genes. The intron arrangements are presented as e.g. 3/-/5, where 3 and 5 indicate the presence of introns 3 and 5, and the dash (-) indicates the absence of intron 4. In some cases information was only avaiable for the region spanning introns 4 and 5, and those are presented as 4/5, etc.

A single sequence from a reliable source was carefully selected for each gene region to represent each species, considering all available sequences for that species. Where available, sequences of ex-type isolates were used (indicated with T in the trees). In some cases, sequences from different sources for the same species were contradictory. When such a contradiction could not be resolved based on careful study of the literature and the origin of isolates, the contradicting sequences were all included in the analyses and are discussed. No sequence that ‘did not fit’ was excluded, and all such taxa are mentioned in the discussion. An additional problem was that for many species only older, shorter DNA sequences were available. When such a short sequence was the only one available, it was included and the missing basepairs (bp) filled with N’s. We were able to include altogether 266 taxa from the *Ophiostomatales* in the various data sets. The LSU data set consisted of 216 taxa, 100 for which only LSU data were available, and thus the latter could not be represented in the other data sets. ITS sequences for altogether 156 taxa were available, of which 50 were only represented by these data. The ITS data were analysed in two separate data sets to improve alignments. Two taxa were represented only by SSU and these were included in the SSU analyses of De Beer *et al.* (2012a). For one species, *L. sibiricum*, no ribosomal sequence data were available, but it could be placed phylogenetically based on its β-tubulin and EF-1α sequences (data not shown). Of the 266 taxa, 22 were undescribed species identified only to genus level based on their morphology, 13 of which were represented only by anamorphs in culture.

Data sets were compiled in MEGA 5.0.5 (Tamura *et al.* 2011). Alignments were done online in MAFFT 6 (Katoh & Toh 2008) using the E-INS-I strategy. The alignment of the ITS data set was subsequently (liberally) treated online with Gblocks (molevol.cmima.csic.es/castresana/Gblocks_server.html) to compensate for substantial variation. Maximum parsimony (MP) was done in PAUP 4.0 b10 (Sinauer Associates, Sunderland, MA), maximum likelihood (ML) was conducted using PhyML 3.0 online (Guindon *et al.* 2010), and Bayesian analyses (BI) were made using MrBayes 3.1.2 (Ronquist & Huelsenback 2003). The most appropriate substitution models for all three gene regions were selected using the Akaike information criterion (AIC) in ModelTest 3.7 (Posada & Crandall 1998) for ML, and MrModelTest 2 (Nylander 2004) for BI. For MP and ML, 1000 bootstrap replicates were performed. For BI four independant runs of 5 million generations each were conducted using duplicate Monte Carlo Markov chain searches with four chains. Trees were saved every 100 generations. For each data set, burn-in was determined using Tracer 1.4 (http://evolve.zoo.ox.ac.uk/software.html).

In the trees resulting from our analyses, we defined species complexes when three or more taxa formed a lineage with significant statistical support in at least one of the analyses, and the included taxa shared morphological and/or ecological characters. Species complexes were named after the oldest and/or best known species in each complex. Lineages not forming part of the major groups, lacking statistical support, or represented by only one or two taxa, as well as species with conflicting generic placement are all discussed below following the major lineages.

MORPHOLOGY

The major lineages in the trees from our analyses correspond largely to key morphological features. Different authors have commonly used different terms for small variations in the same morphological character. For this reason descriptions or tabulated morphological characters without illustrations sometimes leave the impression that certain features are completely different, while they are actually the same or very similar. To simplify the discussion emerging from the phylogenetic analyses, it is necessary to briefly consider the different types of ascomata, ascospores, and anamorphs.

The ascomata in the *Ophiostomatales* are generally short- to long-necked perithecia (in the morphological rather than ontogenetic sense of the term), with a continuum of neck lengths represented in the order (**Fig. 1**), and often a substantial variability in lengths in a single species. The ascospores are produced in evanescent asci, are pushed through the ostiole and carried in a slimy droplet in the case of the long-necked perithecia, most often supported by ostiolar hyphae (**Fig. 1**, e.g. *O. piliferum*). In short-necked perithecia, the ascospores are often longer and produced in an extending, sticky cirrhus of spores protruding through an ostiole surrounded by convergent ostiolar hyphae (**Fig. 1**, e.g. *Cop. concentrica*). A third type of ascomata is cleisthocial, where no neck or ostiole occurs (**Fig. 1**, e.g. *Fragosphaeria reniformis* and *G. aurea*).

We have grouped the ascospores based on morphological features (Figs 2a, b), and included the terminology used in the publications, as indicated. This illustrates that the ascospores of the *Ophiostomatales* mostly belong to one of 11 types (A-K, Figs 2a, b), with three unique forms (C, H, K) each known only from single species. From the illustrations, it is clear that different authors have used different terms describing the same morphology, e.g. in Type A (**Fig. 2**a), the illustrations of ‘allantoid’, ‘orange section’ and ‘curved’ are almost identical. In other cases, the same term is used for vastly different morphotypes (e.g. ‘crescent shaped’ in Types A and F). Where applicable in the discussion, we refer to these morphotype letters rather than choosing any particular term for them. However, these ‘types’ are only meant to ease discussion. For species descriptions, standardized terminology for spore shapes, as illustrated in the The Dictionary of Fungi (Kirk *et al*. 2008), should be applied.

The description of anamorphs is particularly problematic for many species in the *Ophiostomatales* because a continuum of morphological types commonly exists within a single species (Przybyl & De Hoog 1989, Benade *et al.* 1996, 1997, Harrington *et al.* 2001). In some cases, the two extreme forms of such a continuum have been referred to as synanamorphs and were treated in two different genera, e.g. the pesotum- and sporothrix-like anamorphs of *O. quercus* (see De Beer *et al.* 2012b). In other cases, the same anamorph was classified in different accepted anamorph genera by different authors, e.g. the anamorph of *G. clavigera* was treated in *Pesotum* by Okada *et al.* (1998) and in *Leptographium* by Six *et al.* (2003). In line with the current drive towards one fungus one name, De Beer *et al.* (2012b) have followed the format for the description of anamorph states suggested by Cannon & Kirk (2000), which was endorsed by Hawksworth (2011). The anamorphs of the *Ophiostomatales* are thus referred to as sporothrix-, hyalorhinocladiella-, leptographium-, pesotum-, or raffaelea-like, or a combination of two of these terms in cases where intermediate forms exist. Typical examples of each form are presented in **Fig. 3**. The advantage is that these terms are merely descriptive and can thus be used across phylogenetically defined generic boundaries.

DISCUSSION

The results of our analyses confirmed six well-supported lineages representing genera in the *Ophiostomatales* (Figs 4, 5). These included *Ophiostoma s.str., Raffaelea s.str., Ceratocystiopsis, Fragosphaeria, Graphilbum,* and what, for the present time, we refer to as *Leptographium s.l.* The additional species added to our phylogenies have eroded the monophyly of *Ophiostoma sensu* Zipfel *et al.* (2006), and species currently treated in *Ophiostoma* segregated into several distinct lineages. Those lineages not forming part of *Ophiostoma s.str.* or the other genera, including the *S. schenckii-O. stenoceras* complex, and some smaller lineages, are all treated below under *Ophiostoma s.l.*

Ophiostoma sensu stricto

The type species of *Ophiostoma*, *O. piliferum*, grouped in both trees (Figs 4a, 5a) at the centre of *Ophiostoma s.str.* This species is characterized by non-sheathed, orange-section shaped ascospores (Type A, **Fig. 2**a) and a sporothrix-like anamorph (**Fig. 3**). Only one of the other species in *Ophiostoma s.str.*, *O. distortum*, has a similar morphology*,* but the two species did not group together. The majority of the remaining species in *Ophiostoma s.str.* that did not form part of any well-defined species complex in our analyses were previously treated in the 'conifer clade' of the *O. piceae* complex (Harrington *et al.* 2001, Linnakoski *et al.* 2010). These included *O. canum,* type species of the genus *Pachnodium* (Upadhyay & Kendrick 1975)*,* which is therefore treated as a synonym of *Ophiostoma* (De Beer *et al.* 2012b).

The so-called *O. piceae* complex was suggested to be monophyletic and defined by the presence of synnematous pesotum-like anamorphs (**Fig. 3**), in addition to their sporothrix-like anamorphs (Harrington *et al.* 2001), and ascospores similar to those of *O. piliferum* (Type A, **Fig. 2**a). However, in our analyses neither the *O. piceae* complex *sensu* Harrington *et al.* (2001), nor its 'conifer clade' (Linnakoski *et al.* 2010), had phylogenetic support. We thus treat these species as part of *Ophiostoma s.str.* together with several other species with similar morphology, some with pesotum-like anamorphs (*O. araucariae, O. nikkoense, O. ssiori*), and others with hyalorhinocladiella-like anamorphs (*O. brunneum, O. tapionis*). Two more species (*O. allantosporum, O. arduennense*) fit with this group in terms of anamorph-type and ascospore shape, but with the distinction that their ascospores are surrounded by sheaths.

Another group of species, previously referred to as the *O. minus* complex (Gorton *et al.* 2004, Jacobs & Kirisits 2003, Linnakoski *et al.* 2010), could not be defined as a species complex based on our analyses. Included previously in this group were the North American and European forms of *O. minus*, *O. pseudotsugae* (Gorton *et al.* 2004, Linnakoski *et al.* 2010), *O. pseudominus* (Hausner *et al.* 1993b), and *O. kryptum* (Jacobs & Kirisits 2003). These species are characterized by relatively short-necked ascomata (**Fig. 1**), crescent shaped ascospores (Type A, **Fig. 2**a), and hyalorhinocladiella-like anamorphs. Although Linnakoski *et al.* (2010) included *O. tetropii* in the *O. minus* complex in their phylogenetic trees, the 'complex' did not have phylogenetic support and the ascospores of *O. tetropii* differ in morphology from *O. minus* and the other species. *Ophiostoma introcitrinum*, another species with short-necked perithecia, groups close to *O. minus* and *O. pseudominus* in our analyses (**Fig. 4a**) based on a short LSU sequence from Hausner *et al.* (1993b). This species differs from the others by producing a hyaline synnematous anamorph, which was designated as the type species for *Hyalopesotum* (Upadhyay & Kendrick 1975). Based on this placement of *O. introcitrinum,* the genus *Hyalopesotum* is currently treated as a synonym of *Ophiostoma* (De Beer *et al.* 2012b).

All the species mentioned above have varying forms of allantoid to orange section shaped ascospores, two with and the remainder without gelatinous sheaths. The presence of three species with cylindrical ascospores with pronounced rectangular or ossiform sheaths in *Ophiostoma s.str.*, similar to those observed in the *O. ips* complex (Type E, **Fig. 2**a), was thus somewhat surprising. In both trees (Figs 4a, 5a) *O. ainoae* and *O. brunneo-ciliatum* grouped close to *O. floccosum*, while *O. flexuosum* grouped close to *O. canum*. The first two have pesotum-like anamorphs, and can be distinguished from the *O. ips* complex by characteristic spiralling ostiolar hyphae (Mathiesen-Käärik 1954, Solheim 1986). The anamorph of *O. flexuosum* was assigned to *Sporothrix* by Solheim (1986), but the description and the illustrations lack denticles, which means it is probably more appropriately referred to as hyalorhinocladiella-like.

Alignment of β-tubulin sequences of species in *Ophiostoma s.str.*, confirmed that all species for which data were available, had an arrangement of 3/4/-. *Ophiostoma brunneo-ciliatum* was the only exception with -/-/5.

The O. ulmi *complex*

A strongly supported subgroup comprising 15 taxa was present in the ITS tree (**Fig. 5a**). The monophyly is also supported in β-tubulin, where the 14 species for which data were available all share an intron arrangement of 3/4/-. . All the species were isolated from hardwoods, producing Type A ascospores (**Fig. 2**a) and pesotum- and sporothrix-like anamorphs (**Fig. 3**). This group of species was treated as the 'hardwood clade' of the *O. piceae* complex (Harrington *et al.* 2001, Grobbelaar *et al.* 2009, 2010, Linnakoski *et al.* 2010), or even referred to as the *O. quercus* complex (Kamgan Nkuekam *et al.* 2011). However, because *O. ulmi* is the best known species in this clade, and its basionym, *Graphium ulmi*, has the oldest epithet in the clade (Schwarz 1922), we propose that the group be referred to as the *O. ulmi* complex. *Graphium ulmi* was also designated as the type species for the anamorph genus *Pesotum* (Crane & Schocknecht 1973), currently treated as a synonym of *Ophiostoma* (De Beer *et al.* 2012b).

Included in *O. ulmi* complex were four species that do not match the characters of the above-mentioned group. These species have mycelial rather than synnematous anamorphs, with *O. bacillisporum*, *O. torulosum,* and *O. triangulosporium* all producing hyalorhinocladiella-like anamorphs, and *O. undulatum* a sporothrix-like anamorph. The ascospores of *O. undulatum* and *O. torulosum* are of Type A (**Fig. 2**a), while those of *O. bacillisporum* (Type B, **Fig. 2**a) can interpreted as an elongated form of Type A. The ascospores of *O. triangulosporium* are reniform, but have unique, triangular sheaths (Type C, **Fig. 2**a). The latter is the only species that was not isolated from a hardwood host, but rather from the conifer *Araucariae angustifolia* (Butin 1978). The inclusion of *O. triangulosporium* in the *O. ulmi* complex should thus be confirmed with careful re-examination of the type material and more isolates.

The O. pluriannulatum *complex*

One of the lineages with the strongest phylogenetic support in both data sets (Figs 4a, 5a), included 11 species of which eight are morphologically similar to *O. pluriannulatum.* These taxa are characterized by long perithecial necks (**Fig. 1**), up to 8 mm in the case of *O. multiannulatum* (Davidson 1935), producing varying numbers of annuli with swirls of hyphae on the necks (e.g. *O. pluriannulatum,* **Fig. 1**). The non-sheathed, allantoid ascospores (Type A, **Fig. 2**a) are generally slightly longer and narrower than those of other species in *Ophiostoma s.l.* All the species produce sporothrix-like anamorphs (**Fig. 3**).

Two of the species that group in the *O. pluriannulatum* complex based on LSU (**Fig. 4a**), *O. carpenteri* and *O. retusum*, were previously classified in *Ceratocystiopsis* (Upadhyay 1981, Hausner *et al.* 2003) because of their elongated ascospores and short-necked perithecia. However, their ascospores lack the falcate sheaths characteristic of true *Ceratocystiopsis* species (Type F, **Fig. 2**b), and although elongated, they have rounded ends (Type B, **Fig. 2**a). *Ceratocystiopsis* spp. have black ascomata mostly with tapering necks, while these two species have light-coloured ascomata with almost cylindrical necks (e.g. *O. carpenteri,* **Fig. 1**). The two species furthermore have sporothrix-like anamorphs with conidia produced on denticles, similar to all other species in the *O. pluriannulatum* complex. In contrast, *Ceratocystiopsis* spp. have hyalorhinocladiella-like anamorphs with non-denticulate conidiogenous cells.

β-tubulin sequences are presently available only for six species in the *O. pluriannulatum* complex. *Ophiostoma pluriannulatum* and *O. carpenteri* share the typical *Ophiostoma s.str.* arrangement (3/4/-), while the arrangement of *O. longicondiatum*, *O. multiannulatum*, *O. sparsiannulatum*, and *O. subannulatum* is -/-/5 (Zanzot *et al.* 2010).

Several earlier studies mentioned or showed a lineage containing this group of species, without naming the species complex (Hausner *et al.* 1993b, Thwaites *et al.* 2005, Zipfel *et al.* 2006). Villarreal *et al.* (2005) designated it as the *O. multiannualtum* complex, while Kamgan Nkuekam *et al.* (2008b) and Zanzot *et al.* (2010) named it the *O. pluriannulatum* complex. We prefer the latter because *O. pluriannulatum* was the first species in this lineage to be described (Hedgcock 1906).

The O. ips *complex*

The third lineage in *Ophiostoma s.str.* (Figs 4a, 5a) that met our criteria for a well-defined species complex, included 12 species, of which *O. ips* was described first (Rumbold 1931). A thirteenth species, *O. arborea*, could be assigned to the complex based on a SSU sequence (De Beer *et al.* 2012a, **Fig. 3**). *Ophiostoma ips*, together with eight of the species in the complex with known teleomorphs, is characterized by cylindrical ascospores surrounded by a pillow-shaped to ossiform sheath (Type E, **Fig. 2**a). The anamorphs vary between hyalorhinocladiella- to pesotum-like (**Fig. 3**), often forming a continuum between the two forms. *Ophiostoma fuscum* was also included in the clade, and although its teleomorph is not known, it was described appropriately in the genus *Ophiostoma* by Linnakoski *et al.* (2010). Another taxon, yet to be described and known only by its hyalorhinocladiella-like anamorph, also formed part of this complex. Kim *et al.* (2011) referred to this taxon as *Hyalorhinocladiella* sp. B, but because *Hyalorhinocladiella* is a synonym of *Ceratocystiopsis* (see below), we refer to this species as *Ophiostoma* sp. 3 (Figs 4a, 5a).

Ophiostoma japonicum grouped in both trees (Figs 4a, 5a) in a lineage sister to the statistically supported branch that defines the *O. ips* complex. However, because the species fits the morphological characters of the *O. ips* complex, and was also isolated from conifers like all the other species in the complex (Yamaoka *et al.* 1997), it should be included in future studies until its position can be confirmed.

The ex-type isolate of the ambrosial fungus *H. ips* (Harrington *et al.* 2010) also grouped in the *O. ips* complex. Massoumi Alamouti *et al.* (2009) suggested that this fungus represented the anamorph of *O. montium.* β-tubulin sequences of *O. montium* and *H. ips* differ by only 1 bp, and their intron/exon arrangement differs from all the other species in the complex (*O. bicolor, O. fuscum, O. ips*, and *O. pulvinisporum*) with available β-tubulin sequences. These species have an intron arrangement of 2/3/4/-, while *O. montium* and *H. ips* lack all four these introns (-/-/-/-). De Beer *et al.* (2012b) thus formalized the suggested synonymy of the latter two species (Massoumi Alamouti *et al.* 2009).

The only species that apparently does not fit in the complex based on ecology and morphology is *O. tremulo-aureum.* This species was isolated from *Populus* (Davidson *et al.* 1964) and produces crescent-shaped unsheathed ascospores, resembling those of the

O. ulmi complex (Type A, **Fig. 2**a). Thus, its position should be further investigated (De Beer *et al.* 2012b).

Lineage B
This lineage (**Fig. 4a**) lacked statistical support in our LSU analyses, but consists of two smaller, well-supported lineages each comprising of two taxa. All four taxa are ambrosial fungi, two of them described and two undescribed. Although these lineages do not form part of a well-defined species complex, they form part of the well-supported lineage constituting *Ophiostoma s.str.*, which was not only clear in our analyses, but also in those of Rollins *et al.* (2001), Massoumi Alamouti *et al.* (2009) and Harrington *et al.* (2010). The β-tubulin intron arrangement of these species (3/4/-) also correspond with that of *Ophiostoma s.str.* Harrington *et al.* (2010) thus transferred the two known species, *Ambrosiella macrospora* and *A. tingens*, to *Hyalorhinocladiella* based on their affinity with the *Ophiostomatales*, rather than with *Ambrosiella s.str.* in the Microascales, and the fact they are associated with bark beetles, rather than ambrosia beetles (Massoumi Alamouti *et al.* 2009). However, applying the one fungus one name principles, *Hyalorhinocladiella* is now considered a synonym of *Ceratocystiopsis* (see below), and is unavailable for these taxa. Therefore, De Beer *et al.* (2012b) transferred these two species to *Ophiostoma*.

The two undescribed isolates in Lineage B were initially reported as 'dark sterile sp. A' by Krokene & Solheim (1996), who isolated the fungus from *Hylurgops palliatus* infesting spruce in Norway. They were referred to as *Ambrosiella* spp. by Massoumi Alamouti *et al.* (2009) and Harrington *et al.* (2010), but we treat them here as *Ophiostoma* sp. 1 and 2 (**Fig. 4a**).

In conclusion, *Ophiostoma s.str.* is characterized by species with mostly non-sheathed allantoid-like ascospores (Type A, **Fig. 2**a), or cylindrical ascospores with pillow-shaped to rectangular sheaths (Type E, **Fig. 2**a), with sporothrix- and/or pesotum- or hyalorhinocladiella-like anamorphs. Most of these species have loose associations with bark beetles and are associated with sapstain, although some are pathogens of trees (e.g. the Dutch Elm disease fungi).

Unclassified lineages from *Ophiostoma sensu lato*

The S. schenckii - O. stenoceras *complex*
The lineage containing the sequence of *S. schenckii*, the human pathogen and type species for the genus *Sporothrix* (Hektoen & Perkins 1900), also included another human pathogen, *S. luriei*, grouping closest to *S. schenckii* (**Fig. 5a**). Unfortunately no ribosomal DNA sequences were available for the other known human pathogens that form part of this lineage based on other gene regions, *S. globosa* and *S. brasiliensis* (Marimon *et al.* 2007). *Sporothrix schenckii* was for some time treated as the anamorph of *O. stenoceras* (Andrieu *et al.* 1971, Taylor 1970, De Hoog 1974), the oldest species with a known teleomorph in the complex. In a thorough review of all the literature that compared *O. stenoceras* with *S. schenckii*, Summerbell *et al.* (1993) convincingly argued that the two species were distinct. De Beer *et al.* (2003) produced ITS sequences that confirmed this, and showed that they formed part of a lineage that included other species with sporothrix-like anamorphs such as *O. narcissi* (from *Narcissus* bulbs) and *O. abietinum* (erroneously referred to as '*O. nigrocarpum*') from pine. De Beer *et al.* (2003) referred to this lineage as the *S. schenckii-O. stenoceras* complex. More wood-inhabiting species were subsequently added to the complex and are reflected in our phylogenies (Figs 4a, 5a), including *O. gossypinum*, *O. dentifundum, O. fusiforme, O. lunatum*, *O. rostrocoronatum*, and *O. candidum*. All *Ophiostoma* spp. described to date from native *Protea* infructescensces in Southern Africa (see Roets *et al.*, 2012) also form part of this complex, as well as several species associated with soil.

All the species in this lineage with known teleomorphs produce perithecia with medium neck lengths (e.g. *O. splendens*, **Fig. 1**), unsheathed, reniform to allantoid ascospores (Type A, **Fig. 2**a), and sporothrix-like anamorphs (**Fig. 3**). Several of the human pathogenic and soil-associated species, in addition to the normal hyaline conidia, also produce small, pigmented conidia, a character unique to this complex. The only other group producing pigmented conidia, but usually significantly larger, are the ambrosial, raffaelea-like fungi. Furthermore, all species in the *S. schenckii-O. stenoceras* complex for which β-tubulin data are available has an arrangement (-/5) different from the majority of species in *Ophiostoma s.str.* In addition to the phylogenetic separation between *Ophiostoma s.str.* and the *S. schenckii-O. stenoceras* complex*,* these features further distinguish the two groups and suggest that the generic status of the complex needs reconsideration.

The O. tenellum *complex*

This lineage included only three species, *O. tenellum, O. coronatum* and *O. nigricarpum*. Although morphologically similar to species in the *S. schenckii-O. stenoceras* complex, and with a similar arrangement of β-tubulin introns (3/-/5), these three conifer-infesting species were also peripheral to that complex in previous studies (Villarreal *et al.* 2005, Zipfel *et al.* 2006, Linnakoski *et al.* 2010). These species grouped close to Lineage F (see below). For the present we prefer to treat it as part of *Ophiostoma s.l.*

The Raffaelea lauricola *complex*

The lineage (**Fig. 4a**), containing the laurel wilt pathogen, *R. lauricola*, included two other species, *R. brunnea* and an undescribed species, referred to as *Raffaelea* sp. 4. This lineage was also present in the phylogenies produced by Massoumi Alamouti *et al.* (2009) and Harrington *et al.* (2010), but because they included fewer taxa, it grouped close to the *R. sulphurea* complex (see below) and *Raffaelea s.str.* Based on our analyses, this complex does not form part of *Raffaelea s.str.* or any of the other well-resolved genera. These species also differ from *Raffaelea s.str.* and the other complexes in *Ophiostoma* by its β-tubulin intron arrangement of 3/-/-. Perhaps these species need to be treated in another genus, but their generic status and position in the *Ophiostomatales* should await further investigation including more gene regions, before any new combinations are made. We thus treat the complex as part of *Ophiostoma s.l.*

Raffaelea brunnea is the older name of the two described taxa in this lineage (Verrall 1943, Batra 1967), but we suggest that the lineage be referred to as the *R. lauricola* complex. The latter species is widely known as a serious pathogen of the *Lauraceae* in the USA (Harrington *et al.* 2008, 2011, Evans *et al.* 2010, Eskalen & McDonald 2011, Ploetz *et al.* 2011, Shields *et al.* 2011). In common with *R. lauricola*, *R. brunnea* is also associated with ambrosia beetles on hardwoods, namely *Monarthum* spp infesting *Quercus* and *Acer* (Verrall 1943, Batra 1967). The undescribed taxon was isolated from the mycangia of the ambrosia beetle, *Trypodendron rufitarsus,* from lodgepole pines infested by *Dendroctonus ponderosae,* and was reported in the study of Massoumi Alamouti *et al.* (2009).

Smaller lineages

The generic placement of the following lineages will need to be confirmed in future studies. They are best treated in *Ophiostoma s.l.* at present.

Lineage A (**Fig. 4a**) consists of only *O. microsporum*, a species characterized by a sporothrix-like anamorph. The ascospores are of Type A (**Fig. 2**a), but are smaller than most other species in the *Ophiostomatales* (Davidson 1942).

Lineage C (**Fig. 4a**) includes two *Leptographium* spp., *L. brachiatum* and *L. antibioticum*, which grouped apart from other *Leptographium* spp in the ITS2-LSU phylogeny of Jacobs *et al.* (2001b). These two species, both from conifer wood in North America, are morphologically similar and do not grow well on cycloheximide, a feature that typifies most species of *Leptographium s.l.* (Harrington 1988). Although *O. pseudonigrum* groups close to the two *Leptographium* spp. (**Fig. 4a**), the lineage containing all three species had no statistical support. *Ophiostoma pseudonigrum* produces Type E (**Fig. 2**a) ascospores and a hyalorhinocladiella-like anamorph and thus also does not fit with the two *Leptographium* spp. based on morphology.

The well-supported Lineage D (**Fig. 4a**) consists of two species, *O. grande* and *O. ambrosium*. Both species produce Type A (**Fig. 2**a) ascospores. Their anamorphs have respectively been described as sporothrix-like (Samuels & Müller 1978) and raffaelea-like (De Hoog 1974), but although not very clear, the illustrations of the anamorphs show some similarities.

In our LSU analyses (**Fig. 4a**) Lineage E included *O. crenulatum* and *O. fasciatum*, two similar species with short-necked perithecia (**Fig. 1**) and ascospores with falcate sheaths (Type D, **Fig. 2**a) similar to, but shorter than those of *Ceratocystiopsis* spp. No ITS sequence was available for *O. crenulatum*, but in our ITS tree *O. fasciatum* grouped (**Fig. 5a**) with *O. fumeum* and *S. brunneoviolaceae,* although the three species were separated from each other by long branches. Both the latter species were treated as part of the *S. schenckii-O. stenoceras* complex (Madrid *et al.* 2010, Kamgan Nkuekam 2012), although they grouped peripheral to the complex without statistical support. The perithecia of *O. fumeum* are short-necked and show remarkable similarities with those of *O. crenulatum* and *O. fasciatum.* However, while the ascospores of *O. fumeum* correspond in length with those of *O. fasciatum* (without sheath), they lack the falcate sheaths characteristic of the other two species (Olchowecki & Reid 1974, Kamgan Nkuekam 2012). The anamorphs of *O. fumeum* and *S. brunneoviolaceae* are sporothrix-like with prominent denticles, distinguishing them from hyalorhinocladiella-like anamorphs of *O. crenulatum* and *O. fasciatum* (Olchowecki & Reid 1974). Lineage E had some statistical support in both phylogenies, but because of the varying morphology of the four species, we prefer not to define a species complex until further data can support the group.

In the ITS tree (**Fig. 5a**) two species, *O. pallidulum* and *O. saponiodorum*, described by Linnakoski *et al.* (2010), form the well-supported Lineage F. In the analyses of Linnakoski *et al.* (2010), this lineage formed part of a larger well-supported lineage that included what was described above as the *O. tenellum* complex. In our analyses, the two groups are again adjacent to each other (**Fig. 5a**), but without support. The β-tubulin intron arrangements of the two groups also differ, with Lineage F having introns 4/5, and the *O. tenellum* complex -/5.

Lineage G (**Fig. 5a**), accommodating *O. sejunctum* and *O. angusticollis*, shares morphological similarities (Villarreal *et al.* 2005, Griffin 1968) with the *O. tenellum* complex. In common with the phylogeny of Villarreal *et al.* (2005), these two species grouped close to, but distinct from the *O. tenellum* complex.

Ceratocystiopsis

The elongated, sheathed, falcate ascospores (Types F, G, **Fig. 3**) and ascomata with short necks (**Fig. 1**) that characterize *Ceratocystiopsis*, distinguish the genus from all other groups in the *Ophiostomatales*. The genus was treated for a short time as a synonym of *Ophiostoma* (Hausner *et al.* 1993a, Jacobs & Wingfield 2001), but Zipfel *et al.* (2006) showed that it formed a distinct lineage, and re-instated the genus, originally described by Upadhyay & Kendrick (1975). Our analyses (Figs 4a, 5b) support this treatment. Plattner *et al.* (2009) published the first comprehensive study with sequences for most species in the genus, showing that *Cop. minuta,* the type species, consists of several cryptic species. Reid & Hausner (2010) designated an epitype for *Cop. minuta*, fixing the identity of the species. In our analysis, we included the other two unnamed cryptic species as *Cop. minuta* sp. 2 and sp. 3*.* Also included were three more undescribed *Ceratocystiopsis* spp. from Plattner *et al.* (2009) as *Ceratocystiopsis* spp. 1, 2 and 3.

We included LSU data for *Ophiostoma neglectum* in our analyses, confirming that this species also belongs in *Ceratocystiopsis*. Its hyalorhinocladiella-like anamorph (**Fig. 3**) and ascospore morphology (Type H, **Fig. 2**b) is consistent with other species, but the sheathed ascospores are much shorter than those of other species; rather than falcate, they are somewhat cucullate in side view and triangular in face view. The necessary new combination is provided by De Beer *et al.* (2012b).

Another species of somewhat uncertain generic placement is *Cop. longispora.* The morphology of *Cop. longispora*, especially the falcate ascospores (Type F, **Fig. 2**b), resembles *Ceratocystiopsis* species, but it grouped peripheral to members of *Ceratocystiopsis s.str.* in the phylogenies of Hausner *et al.* (1993a), Hausner & Reid (2003), Plattner *et al.* (2009) and Hafez *et al.* (2012). Zipfel *et al.* (2006) did not include *Cop. longispora*, and based on the results of Hausner *et al.* (1993a) and Hausner & Reid (2003), excluded the species from *Ceratocystiopsis*. However, in our trees (Figs 4a, 5b) *Cop. longispora* groups slightly distant from the main body of *Ceratocystiopsis*, but still within a well-supported lineage with those species. We thus follow the suggestion of Upadhyay (1981) and include this species in *Ceratocystiopsis.*

Ceratocystiopsis minuta-bicolor, of which the anamorph (**Fig. 3**) is the type species of *Hyalorhinocladiella* (Upadhyay & Kendrick 1975)*,* groups unambiguously within *Ceratocystiopsis* (Figs 4a, 5b). Under the emended Code, *Hyalorhinocladiella* is thus a synonym of *Ceratocystiopsis* and the generic name can no longer be applied to species outside this lineage. Species residing in other lineages of the *Ophiostomatales* that have been treated in *Hyalorhinocladiella* in the past*,* are discussed under the *O. ips* complex, Lineage B, , the *L. lundbergii* complex and *Graphilbum*.

Fragosphaeria

The genus *Fragosphaeria,* described by Shear (1923), was never associated with the *Ophiostomatales* until Suh & Blackwell (1999), in a study on cleistothecial fungi, discovered that the type species, *F. purpurea*, grouped among some *Ophiostoma* spp. based on SSU and LSU sequences. This placement was confirmed in a four gene phylogeny by Zhang *et al.* (2006). Sequences for the second species in the genus were published by Yaguchi *et al.* (2006), confirming that the two species group together. Only a few subsequent studies included *Fragosphaeria* in rather limited phylogenies of the *Ophiostomatales* (Linnakoski *et al.* 2008, Kolařík & Hulcr 2009, Harrington *et al.* 2010). Our analyses (Figs 4b, 5b) confirmed the monophyly of the two taxa and their distinct generic status in the *Ophiostomatales*.

Of the two species in *Fragosphaeria*, *F. reniformis* was the first described, but in the genus *Cephalotheca* (Saccardo 1881). Shear (1923) later described the genus *Fragosphaeria*, with *F. purpurea* as its type. Gola (1930) and Chesters (1935) treated both species in *Cephalotheca*, but Malloch & Cain (1970) reinstated *Fragosphaeria*, providing the new combination for *F. reniformis*. The two morphological characters that seemingly prevented any previous association with the *Ophiostomatales,* are the cleistothecial ascomata (**Fig. 1**) and the slight pigmentation of the ascospores (Chesters 1935, Stchigel & Guarro 2007). However, the unsheathed, reniform ascospores correspond with the ascospore morphology of most species in *Ophiostoma s.str.* (Type A, **Fig. 2**a). Furthermore, the illustrations by Chesters (1935) show a clear sporothrix-like anamorph (**Fig. 3**) with prominent denticles on the conidiogenous cells of both species. Chesters (1935) described the asci in detail, implying that they are more readily visible than is typical for other genera in the *Ophiostomatales,* but he did mention that they are evanescent, as is the case for all the other ophiostomatalean species. Cleistothecial ascomata are not a unique feature in the *Ophiostomatales*. Four ophiostomatalean species previously treated in *Europhium* (Parker 1957, Robinson-Jeffrey & Davidson 1968), as well as *G. yunnanense* (Yamaoka *et al.* 2008), also produce ascomata lacking necks and ostioles, but all form ascomata with cucullate ascospores and leptographium-like anamorphs. What distinguishes *Fragosphaeria* from other genera in the *Ophiostomatales* is thus not any single character, but the uniqe combination of cleistothecia with slightly pigmented, reniform ascospores, and sporothrix-like anamorphs.

Ecologically, the two *Fragosphaeria* species also fit well within the *Ophiostomatales*. Both are hardwood-inhabiting and associated with stained wood around and inside bark beetle galleries (Shear 1923, Chesters 1935).

Leptographium s.l.

Leptographium was described with the anamorphic *L. lundbergii* as the type species (Lagerberg *et al.* 1927). *Grosmannia* was described only a few years later for sexually reproducing species with sheathed ascospores and leptographium-like anamorphs, including as type species, *G. penicillata* (Goidánich 1936). *Grosmannia* was treated since Siemaszko (1939) as synonym of *Ophiostoma* and later of *Ceratocystis* (Bakshi 1951). In their monograph for *Leptographium*, Jacobs & Wingfield (2001) considered 29 species known only by their anamorphs, together with 17 species with known teleomorphs, which they treated in *Ophiostoma*. Zipfel *et al.* (2006) separated *Grosmannia* from *Ophiostoma* based on a phylogeny of two gene regions and morphological differences. Apart from species with leptographium-like anamorphs, they also showed that several *Ophiostoma* spp. with synnematous anamorphs, not previously linked with *Leptographium* or *Grosmannia*, grouped in a monophyletic lineage among species of these genera (Zipfel *et al.* 2006). The addition of *Leptographium* sequence data in the present study (Figs 4b, 5b), as well as species with synnematous and raffaelea-like anamorphs, shows that the monophyly of the lineage including *Leptographium* and *Grosmannia* spp. is not as strongly supported as previously indicated. Some smaller lineages that were not previously associated with *Leptographium* or *Grosmannia* form part of this group. For the purpose of the present discussion, we refer to the larger lineage as *Leptographium s.l.*, because *Leptographium* is the oldest genus represented.

In recent studies, several species complexes have been defined within *Leptographium s.l.* based on multigene studies, including gene regions not considered here (Lim *et al.* 2004, Massoumi Alamouti *et al.* 2011, Six *et al.* 2011, Duong *et al.* 2012, Linnakoski *et al.* 2012). Although not all of these complexes were equally well-supported in our analyses of rDNA data, we have structured our discussion on this basis. The delineation of most of these complexes is supported by unique intron arrangements of the β-tubulin and EF-1α regions, and these are mentioned for each complex. Species not included in the complexes, are treated below in *Leptographium s.l.*

The L. lundbergii *complex*

The type species of *Leptographium* groups with seven other species (**Fig. 4b**) to form the *L. lundbergii* species complex. The first thorough phylogenetic study of *L. lundbergii* and three of its sister species was undertaken by Jacobs *et al.* (2005). The species complex was redefined and discussed extensively by Linnakoski *et al.* (2012), who added four more recently described species. They also provided the necessary new combination for *Hyalorhinocladiella pinicola* in *Leptographium* (**Fig. 3**). Intron arrangements in the β-tubulin and EF-1α regions are respectively 3/4/- and 3/-. This complex is and will be definitive of any future delineation of *Leptographium*.

The G. clavigera *complex*

The *G. clavigera* complex recently has gained substantial attention because of the close association of *G. clavigera* and *L. longiclavatum* with the ongoing mountain pine beetle (*Dendroctonus ponderosae*) outbreak in Canada and the northwestern states of the USA (Kim *et al.* 2004, Roe *et al.* 2010, Massoumi Alamouti *et al.* 2011). As a result, *G. clavigera* was the first species of the *Ophiostomatales* for which the full genome sequence was released (DiGuistini *et al.* 2007, 2009). Using this genome, Massoumi Alamouti *et al.* (2011) showed with gene genealogies of 15 gene regions of what was initially perceived as a population of *G. clavigera,* actually consisted of two cryptic species, one still undescribed. Six *et al.* (2011) revealed yet another undescribed taxon in the complex, and clarified the confusion that existed as a result of contradictory sequences for ex-type strains of the other species in the complex. In addition to these two undescribed taxa, the complex accommodates the seven species listed in **Fig. 4b**, together with *L. tereforme* (**Fig. 5b**) (Kim *et al.* 2011). It is interesting to note that *G. clavigera* is the type species for the genus *Graphiocladiella* (Upadhyay 1981). *Ophiostoma trinacriforme*, the type species of another genus, *Europhium*, might also form part of the *G. clavigera* complex, but as a result of conflicting sequences, the placement of the species is presently uncertain (see Species 2, *Incertae sedis*, further down).

Species in the *G. clavigera* complex broadly share the same morphology: leptographium-like anamorphs (e.g. *G. aurea*, **Fig. 3**) with relatively short stipes, cleitothecial ascomata (e.g. *G. aurea,* **Fig. 1**) and reniform ascospores with hat-shaped sheaths (e.g. *G. aurea* and *G. clavigera,* Type I, **Fig. 2**b). Intron arrangements for the β-tubulin and EF-1α regions correspond with those of the *L. lundbergii* and *G. piceiperda* complexes.

The L. procerum *complex*

In common with the situation with the *G. clavigera* complex, the *L. procerum* complex attracted research interest in recent years because of the association of *L. procerum* (**Fig. 3**) with the red turpentine beetle, *Dendroctonus valens*. The beetle was introduced into China during the 1980’s, and in combination with *L. procerum*, has caused the death of thousands of native pines (Yan *et al.* 2005, Lu *et al.* 2008, 2009a, b). The complex now includes eight species, seven of them listed in **Fig. 4b**. In their treatment of the complex, Linnakoski *et al.* (2012) showed that *L. sibiricum* also belongs to this group, but no ribosomal sequences of this species were available for the present study. The β-tubulin and EF-1α regions intron arrangements for all species in this complex are respectively 3/4/- and 3/4, except for *L. latens* that lacks intron 4 in EF-1α.

The G. galeiformis *complex*

Grosmannia galeiformis does not produce leptographium-like anamorphs, but synnematous structures appearing to be loose aggregates of leptographium-like conidiomata. Zhou *et al.* (2004c) were the first to show a phylogenetic relationship between *G. galeiformis* and *Leptographium*. A second species, *G. radiaticola,* was subsequently added to the complex Kim *et al.* (2005c). The third species included in the complex based on our ITS phylogeny (**Fig. 5b**), is *Hyalopesotum pini*, which Kim *et al.* (2005c) had confirmed as the anamorph of *G. radiaticola*. Based on β-tubulin and EF-1α sequences, Linnakoski *et al.* (2012) showed that several previous reports of *G. galeiformis* actually represent *G. radiaticola*, but also that there are at least two additional undescribed cryptic species in the complex. Intron arrangements in the β-tubulin and EF-1α regions are respectively -/4/- and 3/4.

The G. olivacea *complex*

The *G. olivacea* complex as defined by Linnakoski *et al.* (2012) and included the first five species present in our LSU analyses (**Fig. 4b**). One of these species, *G. sagmatospora* (**Fig. 3**)*,* is the type species of the anamorph genus *Phialographium* (Upadhyay & Kendrick 1974), currently treated as synonym of *Leptographium s.l.* (De Beer *et al.*

2012b). Our results showed for the first time that *G. vesca* also belongs to this complex. Its synnematous anamorph and cucullate ascospores (Type I, **Fig. 2**b) are consistent with those of other members of the group (Davidson 1958). Based on SSU (**Fig. 3**, De Beer *et al.* 2012a) and ITS data (**Fig. 5b**), *Phialographium erubescens*, known only from its anamorph, also groups in the *G. olivacea* complex. Harrington *et al.* (2001) transferred *Pesotum erubescens* to *Phialographium,* and treated it as the anamorph of *G. cucullata.* De Beer *et al.* (2012b) listed it as a synonym of *G. cucullata*, but suggested that the synonymy need to be reconsidered based on sequences from additional genes. Linnakoski *et al*. (2012) also revealed problems in the delineation of *G. cucullata* and *G. olivaceapini*, that needs to be resolved with further study. Intron arrangements for this complex are the same as for the *G. galeiformis* complex.

The G. piceiperda *complex*

Linnakoski *et al.* (2012) showed that strains identified as *G. piceiperda* separate into five lineages based on β-tubulin and translation elongation factor 1α (EF-1α) sequences, probably representing cryptic species. Two of these lineages might represent *G. piceiperda* and *G. europhioides* (as they are indicated in Figs 4b, 5b), but both species lack ex-type strains and epitypes should be designated. The remaining three lineages in the phylogenies of Linnakoski *et al.* (2012) are not represented in our data sets and probably represent undescribed taxa. Two other known species included in the complex are *G. aenigmatica* and *G. laricis*. All species are characterized by cucullate (Type I **Fig. 2**b) ascospores and typical leptographium-like anamorphs. Intron arrangements for the β-tubulin and EF-1α regions correspond with those of the *L. lundbergii* and *G. clavigera* complexes.

The G. wageneri *complex*

Six *et al.* (2011) included six species in the *G. wageneri* complex. These are also included in our LSU phylogeny (**Fig. 4b**), although not as a supported lineage. Five of the species are associated with root-feeding beetles on conifers in the USA (Jacobs & Wingfield 2001), while one, *L. reconditum*, was isolated from the rhizosphere of wheat in South Africa (Jooste 1978). Two of the taxa are considered host-specific varieties of *G. wageneri* (Kendrick 1962, Harrington & Cobb 1987). Witthuhn *et al.* (1997) was able to distinguish between these varieties based on RAPD profiles. The varieties in this group deserve additional study based on multigene phylogenies. Intron arrangements in the β-tubulin and EF-1α regions are respectively 3/4/- and 3/4.

The G. serpens *complex*

Duong *et al.* (2012) separated what was known as a single species, *G. serpens* with *L. alacris* as synonym, into five species based on a five gene phylogeny. These five species comprise the *G. serpens* complex. They reinstated *Verticicladiella alacris* as *G. alacris*, describing a teleomorph for the species, and described three novel species based on their anamorphs only: *Leptographium castellanum, L. gibbsii*, and *L. yamaokae.* Intron arrangements are the same as those of the *G. wageneri* complex.

The Raffaelea sulphurea *complex*

Four species previously classified in *Raffaelea* (Harrington *et al.* 2010) form a monophyletic lineage in *Leptographium s.l.* in our LSU phylogeny (**Fig. 4b**). This complex includes *R. sulphurea,* the first species to be described (Batra 1967), together with *R. amasae, R. monteteyi*, and *R. quercivora*. Only one of these four species, *R. quercivora*, was represented in the ITS phylogeny (**Fig. 5b**), where it grouped with *R. quercus-mongolicae*, which was not included in the LSU tree. The two lineages present in the LSU tree have β-tubulin intron arrangements different from *Raffaelea s.str.* and the *R. lauricola* complex, but corresponding to most complexes in *Leptographium s.l.* It was 3/4/- for *R. quercivora* and *R. montetyi,* and -/4/- for the other two species. Massoumi Alamouti (2009) also showed that these species formed a lineage distinct from *Raffaelea s.str. Raffaleae* *amasae* (**Fig. 3**) is the type species for *Dryadomyces* (Gebhardt *et al.* 2005), treated by Harrington *et al.* (2010) as synonym of *Raffaelea*. It is clear that these species cannot be accommodated in *Raffaelea s.str.*, but our present phylogenies are not sufficiently robust to show that this lineage represents a genus distinct from *Leptographium*. Assuming that additional data will show that these species represent a novel genus, then *Dryadomyces* would be the appropriate name for it. For the present, these species are retained in *Raffaelea,* but listed under *Leptographium s.l* by De Beer *et al.* (2012b). *Dryadomyces* is listed as a possible synonym (thus with a question mark) under *Leptographium* (De Beer *et al.* 2012b).

Two species in this complex, *R. quercivora* in Japan (Kubono & Ito 2002) and *R. quercus-mongolicae* in Korea (Kim *et al.* 2009), both vectored by ambrosia beetles, were implicated as contributing to the death of large numbers of *Quercus* trees. Similar pathogenicity and vectors are seen among members of the *R. lauricola* complex.

The G. penicillata *complex*

The type species of *Grosmannia*, *G. penicillata* (Figs 1, 2b, 3), formed a strongly supported lineage with 17 other species in both our LSU (**Fig. 4b**) and ITS (**Fig. 5b**) phylogenies, not including the two species of uncertain position labelled with black numbers. The list of corresponds well with the species included by Six *et al.* (2011) and Linnakoski *et al.* (2012) in the *G. penicillata* complex. The EF-1α intron composition was the same (3/-) for all seven species in the complex for which data were available. However, three patterns of β-tubulin introns (3/-/-, 3/4/-, or -/4/5) were observed for the 13 species with data. The species with known teleomorphs all produce allantoid to curved ascospores surrounded by uniform sheaths (Type J, **Fig. 2**b). However, a sequence of the ex-type isolate of *G. pseudoeurophioides,* produced by Hausner *et al.* (1993b, 2000), was also included in the complex based on our LSU phylogeny (**Fig. 4b**). Illustrations from the original description of *G. pseudoeurophioides* (Olchowecki & Reid 1974) clearly show ascospores with distinct cucullate sheaths (Type I, **Fig. 2**b) reminiscent of those in the *G. piceiperda* complex. Jacobs *et al.* (1998, 2000) and Jacobs & Wingfield (2001) considered *G. pseudoeurophioides* a synonym of *G. piceiperda,* based on similarities in the anamorph, not mentioning ascospores. The placement of *G. pseudoeurophioides* in the *G. penicillata* complex is thus suspect and should be reconsidered including additional collections and sequence data.

Lineage I

This lineage (**Fig. 4b**) represents one species, *Esteya vermicola*. The genus and species were described from infected pinewood nematodes (*Bursaphelenchus xylophilus*) in Taiwan (Liou *et al.* 1999). The fungus is characterized by two kinds of conidiogenous cells and conidia. The first kind consists of slightly pigmented, hyalorhinocladiella-like conidiogenous structures and conidia (**Fig. 3**). In contrast, the second type of conidia is adhesive with a unique, lunate shape, produced from flask-shaped phialides and different to all conidiogenous structures known in the *Ophiostomatales*. These conidia readily attach to and infect the nematodes, which then die 8-10 days after infection (Liou *et al.* 1999). The first DNA sequences (used in the present study) were produced by Wang *et al.* (2008), who correctly showed that *E. vermicola* groups among *Grosmannia* and *Leptographium* spp in the *Ophiostomatales*. Several studies followed, considering the potential for this fungus to be used in the biological control of the pinewood nematode (Wang *et al.* 2009, 2010, 2011a, b). The generic placement of this species has not been fully resolved in the current phylogeny (**Fig. 4b**). Its unique biology and morphology suggests that it warrants further study, to enable an appropriate placement within the order.

Raffaelea s.str.

Raffaelea was introduced by von Arx & Hennebert (1965) for a group of anamorphic fungi living in symbiosis with wood-boring ambrosia beetles. In the same paper, they validated a similar genus, *Ambrosiella*, published invalidly by Brader (1964). Over time, several species were added to both genera and some confusion has emerged over the correct placement of these taxa (Batra 1967). Several studies based on DNA sequences confirmed that the two genera are not closely related, with the type species of *Ambrosiella* grouping within the *Microascales* and that of *Raffaelea* in the *Ophiostomatales* (Cassar & Blackwell 1996; Jones & Blackwell 1998). Gebhardt *et al.* (2005) described a second ambrosial genus, *Dryadomyces*, in the *Ophiostomatales*. Massoumi Alamouti *et al.* (2009), using a comprehensive multigene analysis including 56 taxa, showed that *Raffaelea* is polyphyletic in the *Ophiostomatales*, and similarly, *Ambrosiella* in the *Microascales*. Harrington *et al.* (2010) proceeded to make the necessary new combinations in *Raffaelea* for *Ambrosiella* spp. in the *Ophiostomatales*. Some of these emerged in our analyses as Lineage B (**Fig. 4a**) in *Ophiostoma s.str.* and are discussed under that genus above.

Harrington *et al.* (2010) included 55 taxa in their LSU analyses, and 32 in their SSU analyses. This created a deceptive ‘monophyletic’ *Raffaelea* for the remaining ambrosial species. In our analyses (Figs 4, 5) *Raffaelea sensu* Harrington *et al.* (2010) separates into three distinct lineages. The first lineage, well-supported and distinct from other genera, includes the type species for the genus, *R. ambrosiae*, and thus represents *Raffaelea s.str.* (Figs 4a, 5b). The second lineage (**Fig. 4a**) grouped within *Ophiostoma s.l.* and was called the *R. lauricola* complex above, while the third lineage formed part of *Leptographium s.l.* and is referred to as the *R. sulphurea* complex (Figs 4b, 5b) above.

Raffaelea s.str. is characterized by reduced conidiogenous structures (**Fig. 3**), resembling the hyalorhinocladiella-like asexual states in other groups of the *Ophiostomatales*, but often aggregating into sporodochia and producing pigmented conidia (Harrington *et al.* 2010). They are exclusively associated with ambrosia beetles, and have varying β-tubulin intron arrangements: 3/-/5 for *R. tritirachium* and *R. albimanens*, -/4/5 for *R. sulcati*, and 3/4/5 for *R. ambrosiae* and most of the other species.

No *Raffaelea* spp have known teleomorphs. The presence of two *Ophiostoma* spp. with known teleomorphs in *Raffaelea s.str.* in the LSU tree (Fig.4a) should thus be carefully considered, but not discounted. *Ophiostoma deltoideosporum* was isolated from stained pine wood in Canada (Olchowecki & Reid 1974), and is characterized by small perithecia, a reduced hyalorhinocladiella-like anamorph, and cylindrical ascospores with an ossiform sheath (Type E, **Fig. 2**a). The short LSU sequence of the ex-type isolate (Hausner & Reid 1993b), places this species in *Raffaelea s.str.* Similarly, an ITS sequence of *O. deltoideosporum* produced by Mullineux & Hausner (2009) grouped with *R. canadensis* in the lineage representing *Raffaelea s.str.* in our ITS tree (**Fig. 5b**). This placement might be viewed as an anomaly were it not for *O. seticolle,* a species with remarkably similar ascospores, perithecia, and hyalorhinocladiella-like anamorph (Davidson 1966), which grouped in the same lineage (Fig.4a). The latter species was isolated repeatedly from the galleries of an unknown ambrosia beetle on *Tsuga*, suggesting that is has an ambrosial biology (Davidson 1966). Certainly both these species should be considered in future treatments of *Raffaelea*. If their placement in *Raffaelea* can be confirmed, new combinations in *Raffaelea* will need to be provided for them.

Graphilbum

The lineage that is most distinct from the other well-supported genera in the *Ophiostomatales* (Figs 4b & 5b), contains six known species and seven undescribed taxa. Of the known species, *Pesotum fragrans* was the first to be described (Mathiesen-Käärik 1954). The species is known only by its synnematous anamorph (**Fig. 3**). Harrington *et al.*

(2001) recognized that the ex-type isolate did not produce a sporothrix-like synanamorph similar to those of species of *Ophiostoma s.str.* with synnematous anamorphs. Jacobs *et al.* (2003) and Jacobs & Seifert (2004) further characterized the morphology of the species, and included several isolates in their ITS phylogeny. In a more comprehensive phylogeny, Zhou *et al.* (2006) showed that the species grouped very distantly from other *Ophiostoma* and *Leptographium* spp. Kamgan Nkuekam *et al.* (2008b) showed that *O. rectangulosporium*, described earlier by Ohtaka *et al.* (2006), clustered with *P. fragrans*. Our analyses revealed that four more known species grouped in this lineage, including *C. curvicollis* (Olchowecki & Reid 1974), *O. microcarpum* (Yamaoka *et al.* 2004), *O. nigrum* (Davidson 1958), and *O. sparsum* (Davidson 1971). All these species have hyalorhinocladiella- to pesotum-like anamorphs (e.g. *C. curvicollis* and *P. fragrans*, **Fig. 3**), except for *O. rectangulosporium,* for which no anamorph has been observed (Ohtaka *et al.* 2006). The five species that produce teleomorphs all produce ascomata with almost cylindrical, rather than tapering necks of medium lengths (e. g. *O. rectangulosporium*, **Fig. 1**), with cylindrical ascospores with ossiform sheaths (Type E, **Fig. 2**a).

The anamorph of *O. sparsum* is the type species of the genus *Graphilbum,* which was described to accommodate hyaline synnematous anamorphs of *Ophiostoma* (at the time treated as *Ceratocystis*) (Upadhyay & Kendrick 1975). Although the anamorphs of *O. ips, O. montium* and *O. japonicum* were later described as *Graphilbum* spp. (Upadhyay 1981, Hutchison & Reid 1988, Yamaoka et al. 1997, Kim et al. 2003), no other species were ever described in the genus. The synonymy of *Graphilbum* with *Pesotum* suggested by Okada *et al.* (1998) was widely accepted (e.g. Hausner *et al*. 2000, Zipfel *et al*. 1996). However, the type species of *Pesotum*, *O. ulmi*, groups within *Ophiostoma s.str.,* which means that *Pesotum* is treated under the new Code as synonym of *Ophiostoma* (De Beer *et al.* this 2012b). The fact that *O. sparsum* groups in a lineage distinct from *Ophiostoma s.str.*, releases the name *Graphilbum* from its synonymy with *Pesotum*, and makes it available for species in this lineage. The one fungus one name principles make it possible to redefine what was previously considered an anamorph name for application to species with known teleomorphs. De Beer *et al*. (2012b) thus re-instated the name *Graphilbum*, redefined the genus to accommodate teleomorphs, and transferred *P. fragrans*, *C. curvicollis*, *O. nigrum* and *O. microcarpum* to this genus.

Several other studies introduced taxa grouping with *P. fragrans* based on sequences, but without describing the species. These taxa are all known only as anamorphs, and were referred to various genera in various publications. We included these in our phylogenies, referring to them as numbered species of *Graphilbum*. *Graphilbum* sp. 1 (**Fig. 3**, De Beer *et al.* 2012a) comes from Ecuador and was reported as a *Pesotum* sp. in the study of Geldenhuis *et al.* (2004). *Graphilbum* sp. 2 (**Fig. 3**, De Beer *et al.* 2012a) and *Graphilbum* sp. 3 (**Fig. 4b**) were reported from Canada, respectively as an *Ophiostoma* (Hafez *et al.* 2012) and an *Ambrosiella* sp. (Kim *et al.* 2005b). *Graphilbum* spp. 4 and 5 (Figs 4b & 5b) from California, as respectively *Hyalorhinocladiella* sp. A and ‘sterile fungus’ by Kim *et al.* (2011). *Graphilbum* sp. 6 (**Fig. 5b**) were reported from China (Lu *et al.* 2009a), and *Graphilbum* sp. 7 from Spain (Romón *et al.* 2007), both as *‘O. rectangulosporium*-like’. Lastly, Thwaites *et al.* (2005) reported a *Pesotum* sp. from Australia, labelled in our tree (**Fig. 5b**) as *Graphilbum* sp. 8.

Incertae sedis

The generic placement of the *S. lignivora* complex, Lineage H and the species indicated with numbers in black circles in our phylogenetic trees (Figs 4, 5) is uncertain. For the species listed below, different sequences of the same species resulted in conflicting phylogenetic placements. The taxonomic position of all of these taxa needs to be confirmed in studies that include ex-type isolates and analyses of sequences for additional gene regions.

The S. lignivora *complex*

In a study of sporothrix-like fungi isolated from wooden utility poles, De Meyer *et al.* (2009) described amongst others, *Sporothrix lignivora*, a species that grouped in their phylogeny peripheral to the *S. schenckii-O. stenoceras* complex. The study of Linnakoski *et al.* (2010) and the results of this study (Figs 4b, 5b) confirmed that the species forms a distinct lineage. The β-tubulin introns (-/4/5) of *S. lignivora* also differ from those of other *Sporothrix* spp. in the *S. schenckii-O. stenoceras* complex. Our ITS tree (**Fig. 5b**), furthermore, shows that two undescribed taxa form a well-supported lineage together with *S. lignivora*. These taxa were respectively reported as *Sporothrix* sp. 2 from *Thuja* in Canada (Lim *et al.* 2005a), and *Sporothrix* sp. in a metagenomic study on the fungal endophytes of *Yucca* roots in the USA (Khidir *et al.* 2010). The distance with which this complex groups from other genera and complexes in the *Ophiostomatales*, suggests that it might represent a new genus. Until more material and data are available, we treat the complex as of uncertain affiliation.

Lineage H

A single taxon, *O. grandicarpum*, formed Lineage H (**Fig. 5b**), which were close to, but not part of the *S. lignivora* complex. This species also resembles species in the *O. tenellum* complex and Lineages F and G, and grouped close to these in the smaller ITS phylogeny of Villarreal *et al.* (2005). *O. grandicarpum* should be considered together with both the *O. tenellum* and *S. lignivora* complexes in future taxonomic studies.

Species 1

The placement of *O. seticolle* in *Raffaelea s.str.* based on its LSU sequence (**Fig. 4a**) is discussed above. However, ITS data of ex-type isolate (CBS 634.66) from Jacobs *et al.* (2003) place this species close to *O. rostrocoronatum* in the *S. schenckii-O. stenoceras* complex (**Fig. 5a**), from which it differs significantly in morphology. The ex-type isolates must be obtained from both collections again and studied morphologically to determine whether they still corresponds with the original description (Davidson 1966), before new sequences are produced.

Species 2

Hausner *et al.* (1992, 2000) showed that *O. trinacriforme* (CFB 527) grouped in *Grosmannia,* close to *G. aurea* based on SSU sequences. However, in the analyses of De Beer *et al.* (2012a, **Fig. 3**) their sequence fell between *Ophiostoma* and *Ceratocystiopsis*. The LSU sequence of the same strain (Hausner *et al.* 2000) was placed in the *O. ips* complex in our analyses (**Fig. 4a**), while the sequence of *O. trinacriforme* (CBS 210.58 = CMW 670) produced by Jacobs *et al.* (2001b) grouped with *O. stenoceras* in the *S. schenckii-O. stenoceras* complex. None of these discordant placements correspond with the morphological characters, such as cleistothecia, cucullate ascospores (Type I, **Fig. 2**b), and the leptographium-like anamorph originally described for *O. trinacriforme* (Parker 1957, Jacobs & Wingfield 2001), which suggest a placement in the *Grosmannia clavigera* complex. For the present, the generic placement of the species must be considered uncertain.

Ophiostoma trinacriforme is the type of the genus *Europhium*. Therefore, it is appropriate to consider our current understanding of the status of *Europhium* here. Subsequent to its description (Parker 1957), the majority of authors recognised *Europhium* as a distinct genus because of its cleistothecial ascomata (Müller & von Arx 1973, von Arx 1974, 1981, Redhead & Malloch 1977, von Arx & Van der Walt 1987, Barr 1990). De Hoog (1974) was the first to treat *Europhium* as synonym of *Ophiostoma,* while Upadhyay & Kendrick (1975), and Upadhyay (1981, 1993) treated it as a synonym of *Ceratocystis s.l.* Most recently, Zipfel *et al.* (2006) listed *Europhium* as synonym of the reintroduced *Grosmannia,* to which they transferred the three other *Europhium* species (Robinson-Jeffrey & Davidson 1968). All three of these species are now treated in the *G. clavigera* complex. However, the unresolved generic placement of *E. trinacriforme* calls to question the suggested synonymy of *Europhium* with *Grosmannia*. For the present, *Europhium* is listed as a possible synonym under *Grosmannia* in the nomenclator compiled by De Beer *et al.* (2012b).

Species 3
The LSU sequence for the ex-type strain of *O. brevicolle* (CBS 795.73 = CMW 447 = ATCC 12971) from Jacobs *et al.* (2001b) placed this species close to *O. bragantinum* in the *S. schenckii*-*O. stenoceras* complex in our analyses (**Fig. 4a**). However, Hausner *et al.* (2000), Mullineux & Hausner (2009), and Hafez *et al*. (2012) produced LSU, ITS and SSU sequences, respectively, for another isolate of *O. brevicolle* (CBS 150.78 = CMW 474), that placed this species close to the *G. olivacea* complex (Figs 4b, 5b), where its morphology (Davidson 1958) suggests it might more appropriately group.

Species 4
ITS sequences for two strains (UM 110, UM 113) generated for *Cop. rollhanseniana* by Plattner *et al.* (2009) are identical and group close to *G. galeiformis* (**Fig. 5b**). The LSU and β-tubulin sequences (data not shown) of the same strains group within *Ceratocystiopsis,* which is probably correct. Their LSU sequences also correspond to that of the ex-type isolate (CBS 118669 = UAMH 9774 = CMW 13791) produced by Zipfel *et al.* (2006), forming part of *Ceratocystiopsis* (**Fig. 4a**). Despite these contradictory sequences, we believe the placement of *Cop. rollhanseniana* in *Ceratocystiopsis* is correct.

Species 5
LSU sequences for *G. francke-grosmanniae* from the studies of Hausner *et al.* (2000) (ex-type ATCC 22061), Jacobs *et al.* (2001b) (ex-type CMW 445), and Zipfel *et al.* (2006) (CMW 2975), gave different results in our analyses. The sequence by Hausner *et al.* (2000) grouped between the *L. procerum* and *G. galeiformis* complexes (**Fig. 4b**), that of Zipfel *et al.* (2006) between the *G. wageneri*- and *G. serpens*-complexes, and the one by Jacobs *et al.* (2001b) in the *G. penicillata*-complex. An ITS sequence of ATCC 22061 produced by Mullineux & Hausner (2009) grouped close to the *G. olivacea* complex (**Fig. 5b**). The treatment of this species in *Grosmannia* by Zipfel *et al.* (2006) remains the most acceptable for the present, but the correct placement of the species within *Leptographium s.l.* needs to be determined.

Species 6
ITS and LSU sequences for the ex-type strain of *L. guttulatum* (CMW 742) were produced by Jacobs *et al.* (2001a) and Jacobs *et al.* (2001b), respectively. However, *L. guttulatum* is placed differently in the two phylogenies, in the *G. clavigera* complex by ITS (**Fig. 5b**) and *G. penicillata* (**Fig. 4b**) complex with LSU.

CONCLUSIONS

The present study is the first review of the taxonomy of the *Ophiostomatales* since 1993 (Wingfield *et al.* 1993), and it attempts to assess and condense the impact of 20 years of DNA sequencing on the taxonomy for this group of fungi. The most extensive ribosomal DNA data sets for the *Ophiostomatales* to date were assembled and data for 266 taxa were analysed. The resulting phylogenies confirmed the delineation of six genera, 17 species complexes and eight minor lineages. They also revealed new relationships and showed that some lineages previously believed to be monophyletic are not so.

Careful comparison of the phylogenetically defined genera and species complexes with the many species groups and sections from studies predating DNA sequences, verified that not a single one of the previously defined morphological groups accurately predicted the present phylogenetic lineages. In the older studies, groups were most often based on a single common morphological character, e.g. ascospore shape (Upadhyay 1981), while the phylogenetically defined genera and species complexes emerging in this study were in almost all cases supported by a unique combination of ascomatal morphology, ascospore shape, ecological niche, and β-tubulin and EF-1α intron arrangements. Although anamorph morphology was broadly reflected by the major groups, substantial overlap between anamorph types made this feature less valuable in defining groups. Most of the morphological characters evolved more than once in the *Ophiostomatales*, e.g. cylindrical ascospores with pillow shaped sheaths (Type E, **Fig. 2**a) characterize both the *O. ips* complex and *the* newly defined genus *Graphilbum*. Similarly, raffaelea-like ambrosial fungi are present in at least three lineages. The result is that none of the phylogenetically defined groups can be identified based on only one morphological character. Clearly, phylogenetic analyses of DNA sequences are absolutely indespensable to resolve relationships between taxa at all levels in this order.

The movement towards a one fungus one name for fungal systematics that resulted in the emended nomenclatural Code (Hawksworth 2011, McNeill *et al.* 2011), has emerged from the clarity that phylogenetic analyses has provided. Over a relatively long period of time, five teleomorph genera and 12 anamorph genera had been described in the *Ophiostomatales*. Under dual nomenclature, it was accepted that *Ophiostoma* accommodated *Ophiostoma*, *Pesotum*, *Hyalorhinocladiella* and *Sporothrix* spp. Based on phylogenetic inference we are now able to confidently delineate five genera in the *Ophiostomatales*. However, under the new Code the oldest name in any lineage including the type species of more than one genus, will have priority, with the other names as synonyms, irrespective of morph. In the *Ophiostomatales,* three of the currently accepted genera are defined by names previously reserved for species with known teleomorphs (*Ophiostoma, Ceratocystiopsis, Fragosphaeria*), while the other three (*Leptographium, Raffaelea, Graphilbum*) were previously considered anamorph genera. In our analyses the type species of seven other genera (*Grosmannia, Europhium, Sporothrix, Phialographium, Graphiocladiella, Dryadomyces,* and *Esteya*) did not group in the same species complexes as the type species of the genera in which those seven species are currently treated. E.g. *Phialographium sagmatospora* in the *G. olivacea* complex represents *Phialographium*, but *Ph. sagmatospora* is currently treated in *Grosmannia*, of which the type species, *G. penicillata,* stands at the centre of the *G. penicillata* complex. The last five of the seven genus names are typified by anamorphic species and were thus not available for species with known teleomorphs. Under the emended Code, these names have in effect been ‘released’ to be used irrespective of morph, and are now available should some of these lineages be elevated to genus level. We have discussed the impact that these changes will have on the various genera and species complexes in the *Ophiostomatales* in the immediate future. We have also made some recommendations (**Boxes 1 & 2**), especially for dealing with taxa in the interim, in cases where generic boundaries are not fully resolved, to avoid indiscriminate name changes.

The present study provides a foundation for future taxonomic studies in the *Ophiostomatales*. Many species complexes have been redefined, and the newly added species should be incorporated in future studies dealing with these complexes. A priority should be to clarify the generic status of the species complexes currently treated in *Ophiostoma s.l.* and *Leptographium s.l.* to facilitate appropriate new combinations for these species.

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Box 1 Recommendations to ensure nomenclatural stability in *Ophiostoma s.l.*

If the recommended one fungus one name principles (Hawksworth 2011, McNeill *et al.* 2011) are applied indiscriminately and with immediate effect to *Ophiostoma s.l.* as defined in this study, *Sporothrix* will have priority as the oldest valid genus in the group. The result would be a redefined *Sporothrix* containing 147 species, 104 requiring new combinations, including well-known, economically important species like *O. ulmi* and *O. novo-ulmi*. We recommend a more conservative and phylogenetically defensible approach whereby *Ophiostoma s.str.* is maintained with *O. piliferum* as type species. All new species and combinations needed in *Ophiostoma s.str.* should be described as *Ophiostoma*, even in the absence of a teleomorph, as has already been done for species like *O. fuscum* and *O. tapionis* (Linnakoski *et al.* 2010), and *O. australiae*, *O. cupulatum*, *O. macrosporum*, and *O. tingens* (De Beer *et al.* 2012b).

The remaining complexes and lineages in *Ophiostoma s.l.* should be reconsidered carefully to determine their generic status. For the interim we recommend the following:

1. maintain species currently treated in *Ophiostoma* (33 taxa not part of *Ophiostoma s.str.*), *Sporothrix* (36 taxa), *Leptographium* (2 taxa), and *Raffaelea* (2 taxa) in those genera;
2. describe new species in *Ophiostoma*, irrespective of morph.

The result of this approach will be that currently known species in *Ophiostoma s.l.* (excluding *Ophiostoma s.str.*) will be transferred to appropriate genera once those are delineated. Many inappropriate new combinations that will need to be corrected later will be avoided following this approach. Although species newly described in the foreseeable future in *Ophiostoma s.l.* will probably have to be transferred to other genera at a later stage, these would be far fewer than if the 80 known species are transferred now and then maybe again later.

Box 2 Recommendations to ensure nomenclatural stability in *Leptographium s.l.*

Subsequent to the publication of Zipfel *et al.* (2006), species in *Leptographium s.l.* producing teleomorphs were described in *Grosmannia* (Lu *et al.* 2009a, Duong *et al.* 2012, Masuya *et al.* 2012), and those presenting only anamorphic structures in *Leptographium* (Lu *et al.* 2008, Zhou *et al.* 2008, Jacobs *et al.* 2010, Paciura *et al.* 2010a, Kim *et al.* 2011). In applying single name nomenclature, *Leptographium* would take priority as the older of the two genera. The implication is that 37 *Grosmannia* species need to be transferred to *Leptographium*, 20 requiring new combinations. As illustrated by our analyses, *Leptographium s.l.* may include several smaller genera that are not yet satisfactorily delineated by existing sequence data. The only way to resolve the position of these taxa will be an extensive multigene phylogeny including several genes and strains representative of all the major lineages. New combinations made now may be superceded by the recognition of additional segregate genera in the forseeable future. To avoid such taxonomic redundancy, we suggest that for the interim species of *Leptographium s.l.* be treated as follows:

The remaining complexes and lineages in *Ophiostoma s.l.* should be reconsidered carefully to determine their generic status. For the interim we recommend the following:

1. maintain all species currently treated in *Leptographium* and *Grosmannia* in those genera;
2. treat all new species and combinations forming part of *Leptographium s.l.,* apart from those grouping the *G. penicillata* complex, in *Leptographium*, irrespective of their morph or anamorph structures*;*
3. describe new species in the *G. penicillata* complex in *Grosmannia,* irrespective of their morph;
4. treat the current species and new taxa to be described in the *R. sulphurea* complex in *Raffaelea*;
5. maintain *Esteya vermicola* in *Esteya*.

De Beer *et al.* (2012b) applied these recommendations to two species producing teleomorphs treated in *Ophiostoma* that belong to *Leptographium s.l.* The two species, *O. verrucosum* and *O. obscurum*, typically would have been transferred to *Grosmannia*, but based on our second recommendation are now treated in *Leptographium*.

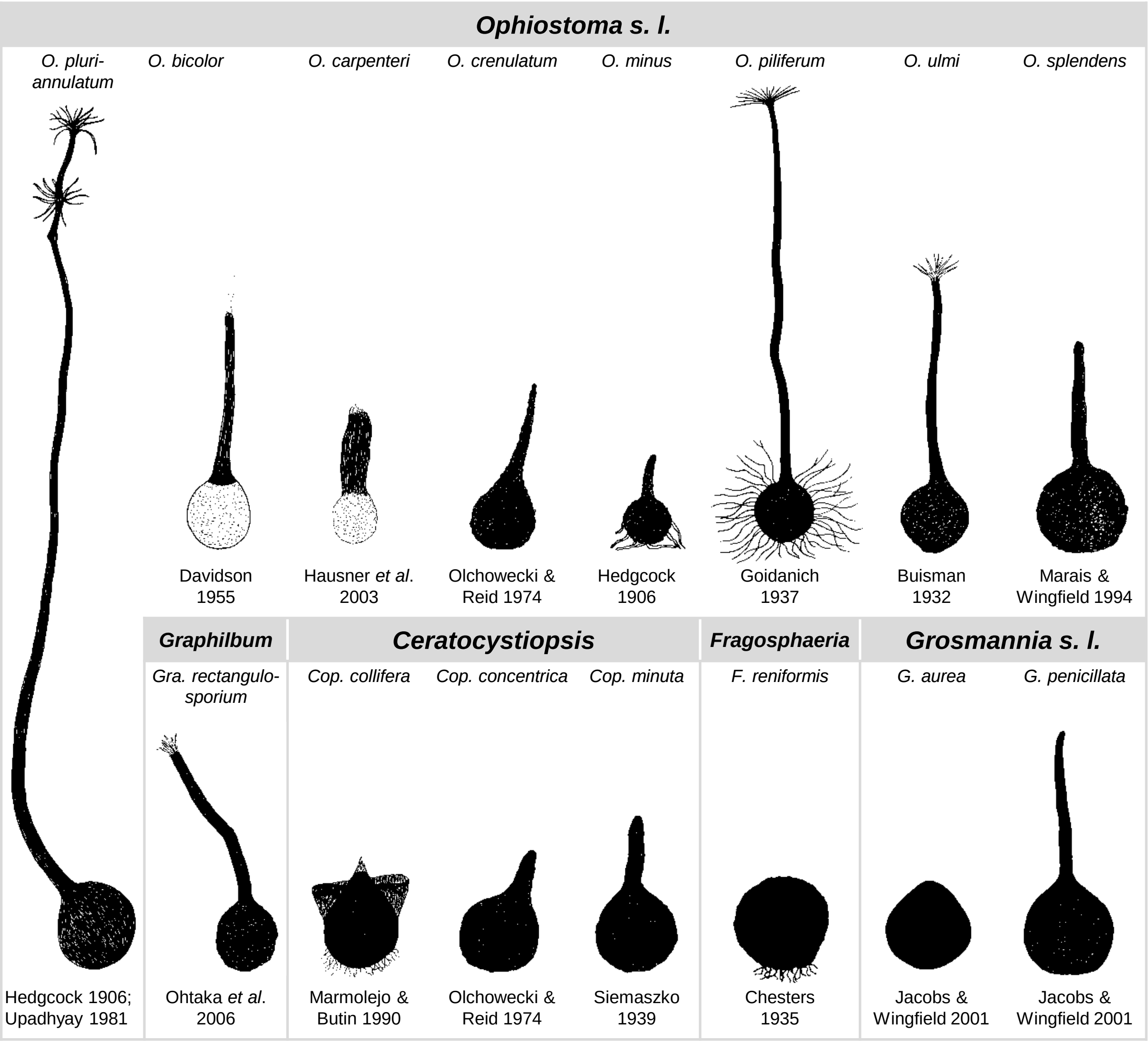


Fig. 1 A selection of ascomata representing the variety of forms produced by species of the *Ophiostomatales*, redrawn from illustrations in publications as indicated.

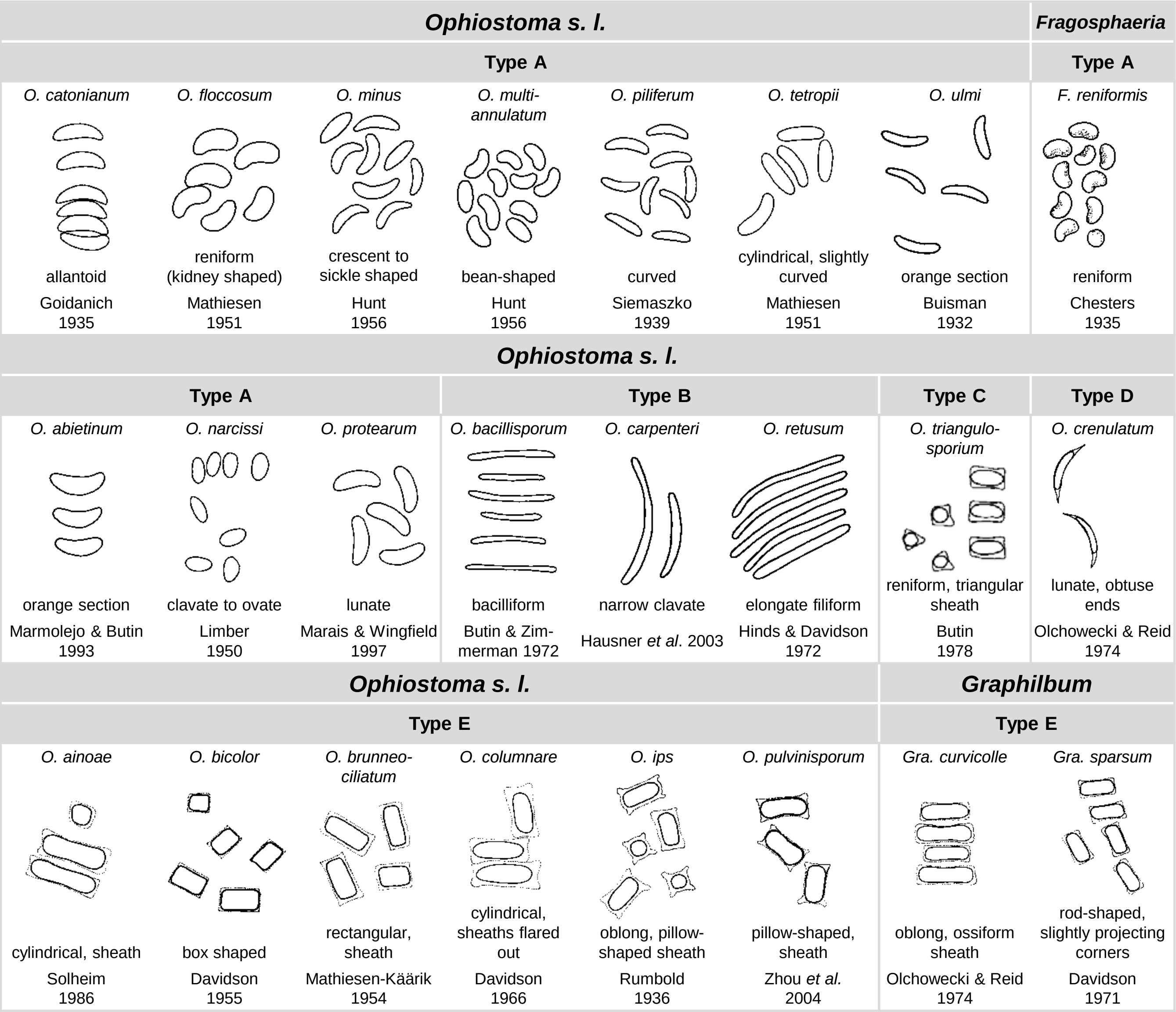
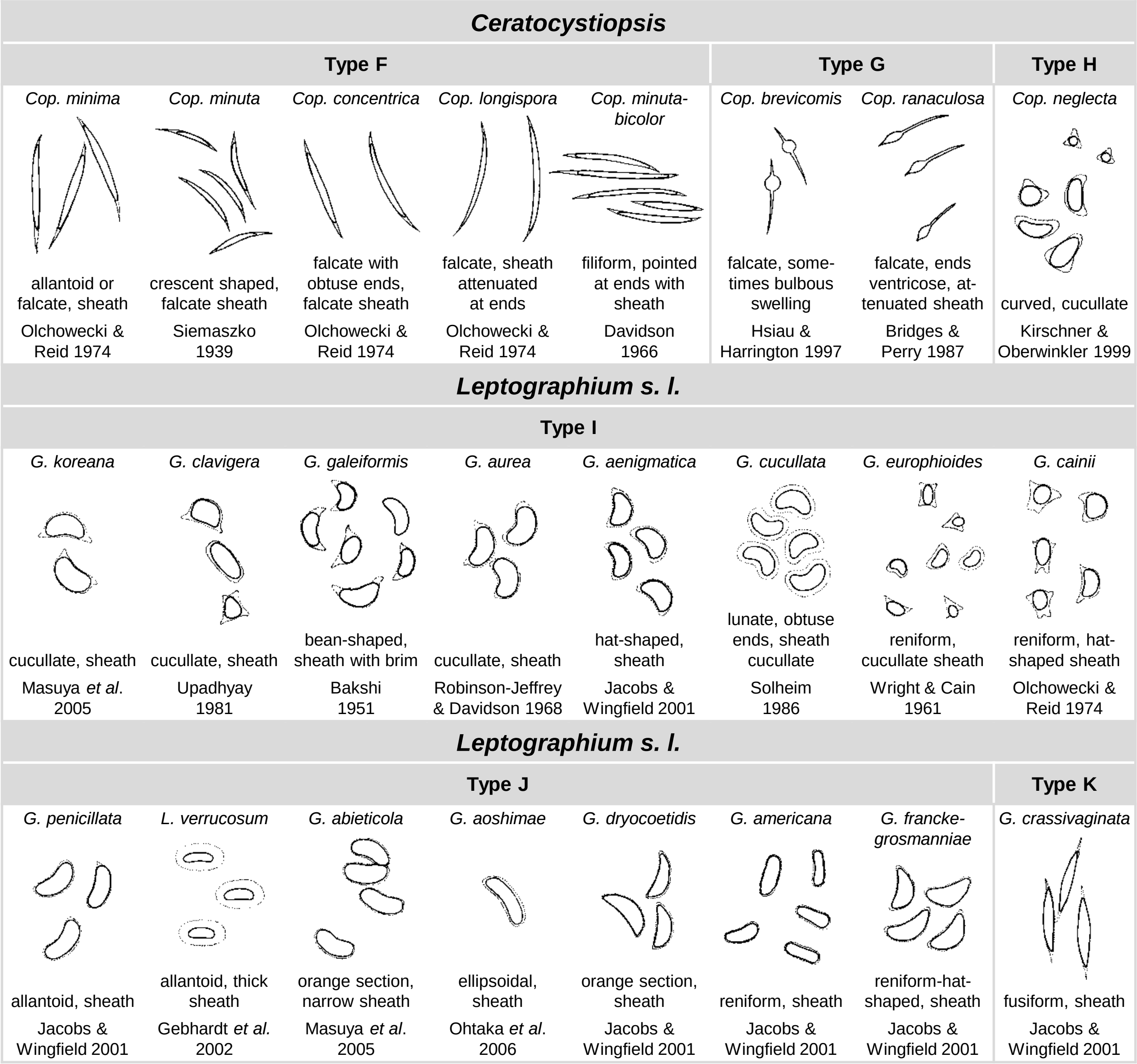


Fig. 2a A representative selection of ascospores produced by species of the *Ophiostomatales*, redrawn from illustrations in publications as indicated. The spores are grouped into types based on shape and the presence or absence of gelatinous sheaths.



Ceratocystiopsis

Type F					Type G		Type H
Cop. minima	*Cop. minuta*	*Cop. concentrica*	*Cop. longispora*	*Cop. minuta-bicolor*	*Cop. brevicomis*	*Cop. ranaculosa*	*Cop. neglecta*
allantoid or falcate, sheath	crescent shaped, falcate sheath	falcate with obtuse ends, falcate sheath	falcate, sheath attenuated at ends	filiform, pointed at ends with sheath	falcate, sometimes bulbous swelling	falcate, ends ventricose, attenuated sheath	curved, cucullate
Olchowecki & Reid 1974	Siemaszko 1939	Olchowecki & Reid 1974	Olchowecki & Reid 1974	Davidson 1966	Hsiau & Harrington 1997	Bridges & Perry 1987	Kirschner & Oberwinkler 1999

Leptographium s. l.

Type I							
G. koreana	*G. clavigera*	*G. galeiformis*	*G. aurea*	*G. aenigmatica*	*G. cucullata*	*G. europhioides*	*G. cainii*
cucullate, sheath	cucullate, sheath	bean-shaped, sheath with brim	cucullate, sheath	hat-shaped, sheath	lunate, obtuse ends, sheath cucullate	reniform, cucullate sheath	reniform, hat-shaped sheath
Masuya *et al*. 2005	Upadhyay 1981	Bakshi 1951	Robinson-Jeffrey & Davidson 1968	Jacobs & Wingfield 2001	Solheim 1986	Wright & Cain 1961	Olchowecki & Reid 1974

Leptographium s. l.

Type J							Type K
G. penicillata	*L. verrucosum*	*G. abieticola*	*G. aoshimae*	*G. dryocoetidis*	*G. americana*	*G. francke-grosmanniae*	*G. crassivaginata*
allantoid, sheath	allantoid, thick sheath	orange section, narrow sheath	ellipsoidal, sheath	orange section, sheath	reniform, sheath	reniform-hat-shaped, sheath	fusiform, sheath
Jacobs & Wingfield 2001	Gebhardt *et al.* 2002	Masuya *et al*. 2005	Ohtaka *et al*. 2006	Jacobs & Wingfield 2001	Jacobs & Wingfield 2001	Jacobs & Wingfield 2001	Jacobs & Wingfield 2001

Fig. 2b A representative selection of ascospores produced by species of the *Ophiostomatales*, redrawn from illustrations in publications as indicated. The spores are grouped into types based on shape and the presence or absence of gelatinous sheaths.

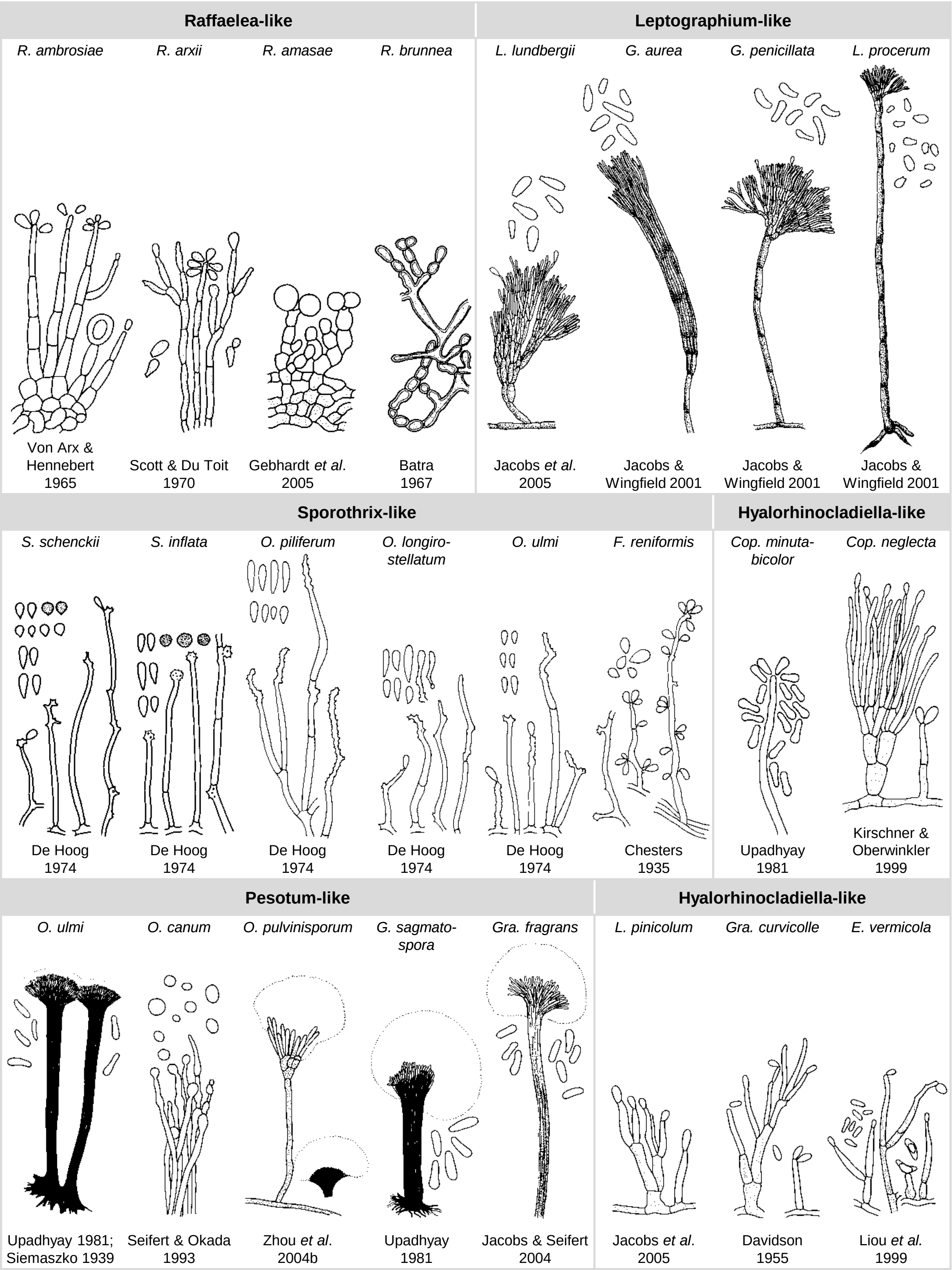
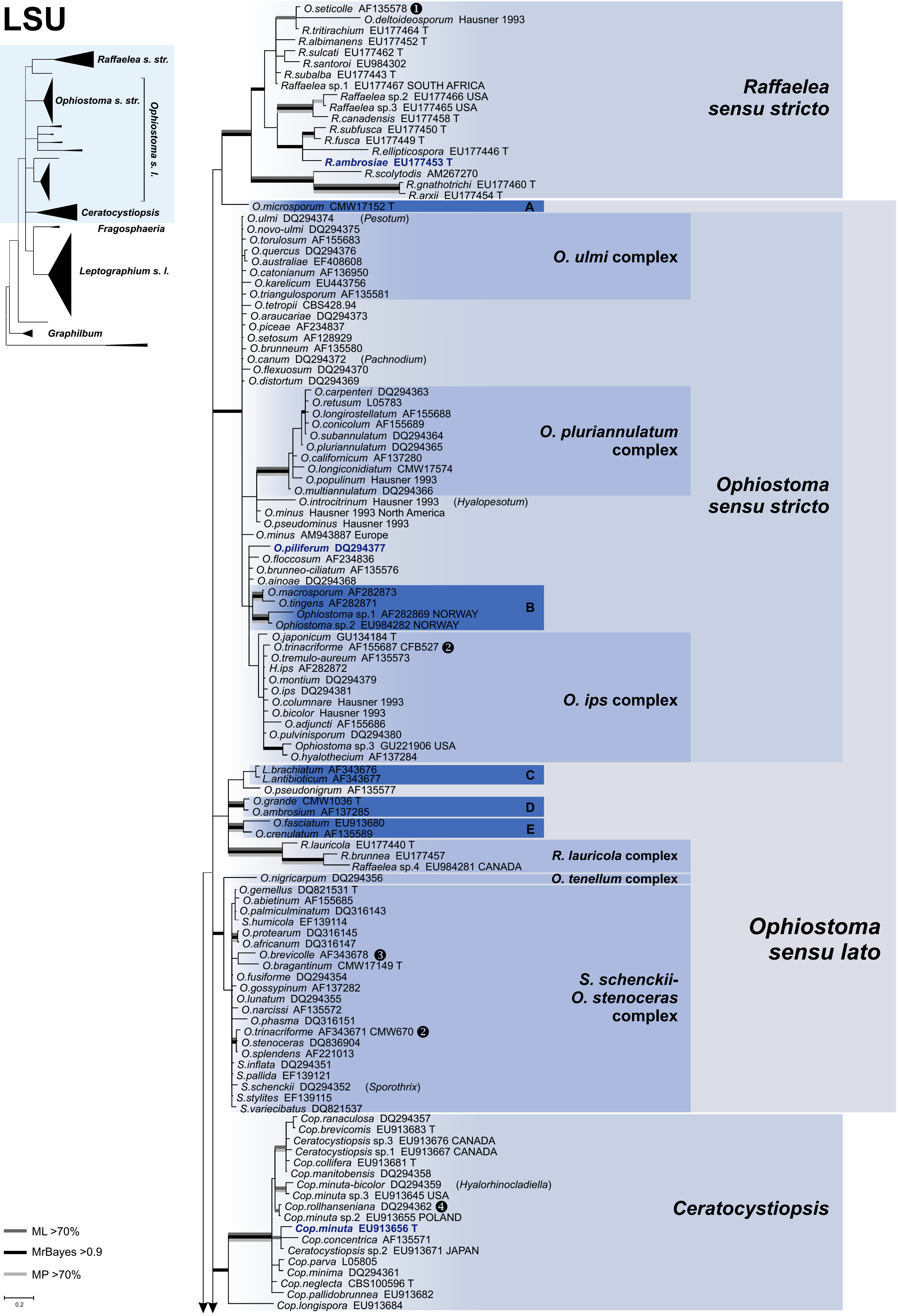
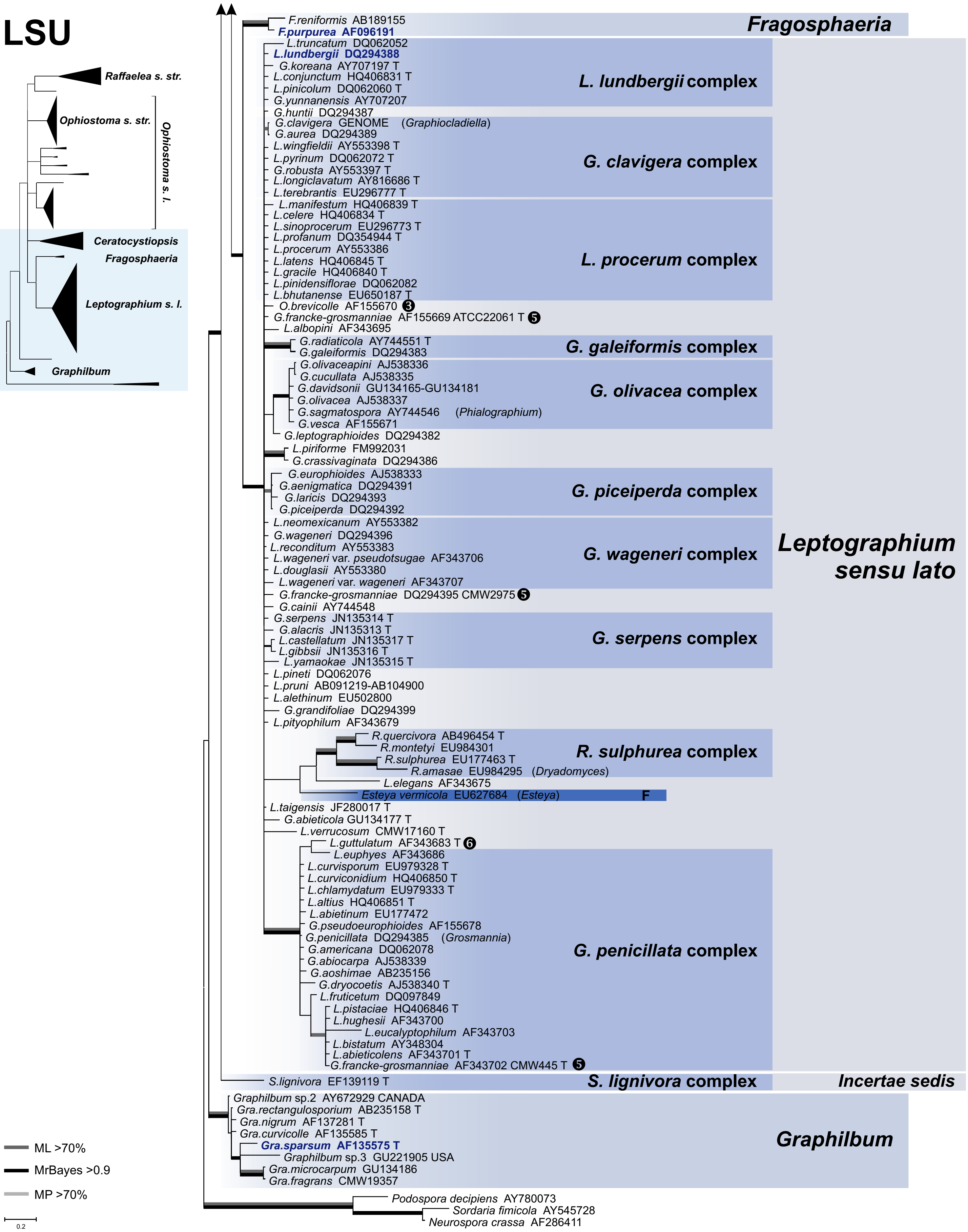


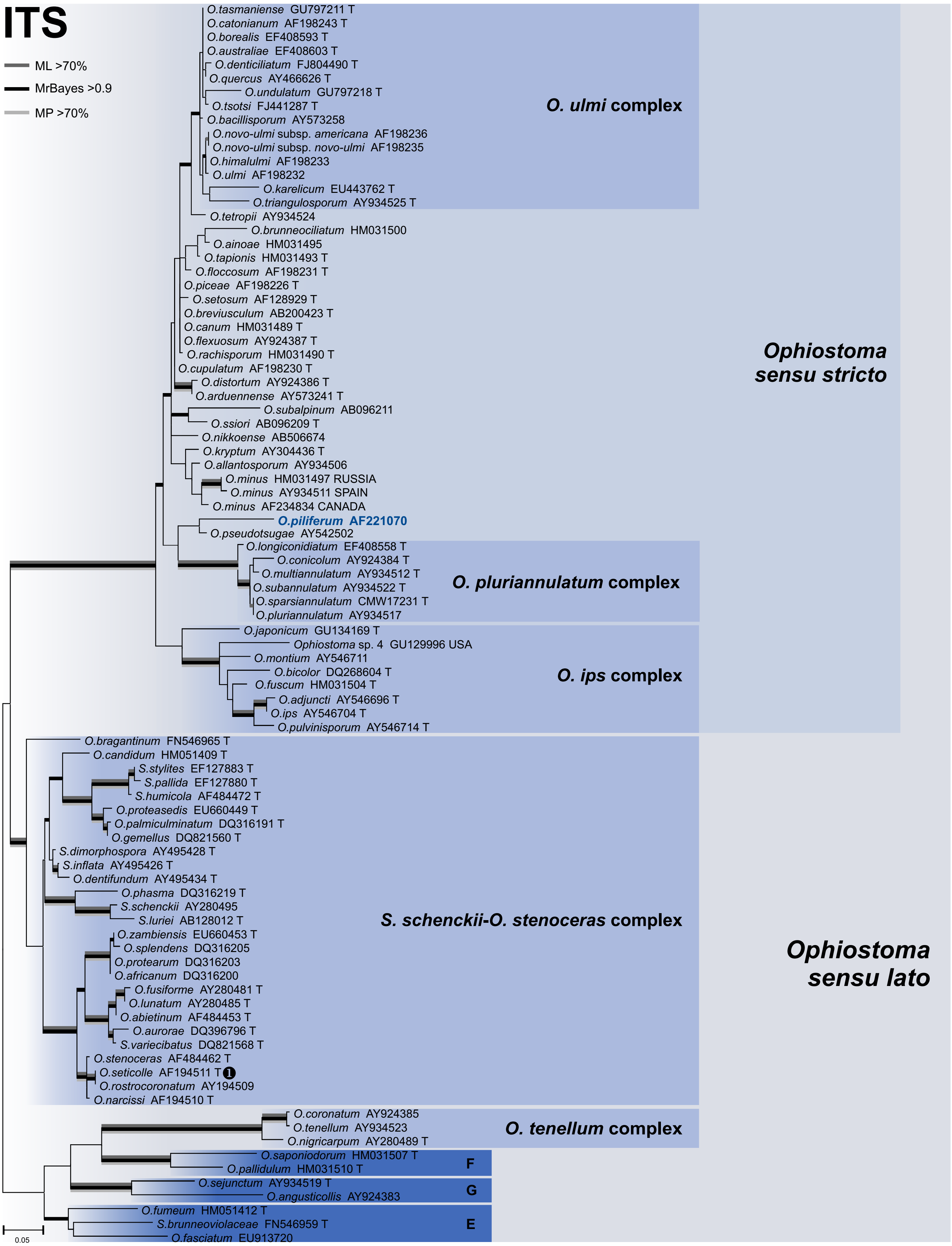
Fig. 3 The asexual forms of the *Ophiostomatales*, redrawn from illustrations in publications as indicated and broadly categorized based on conidiogenous structures.

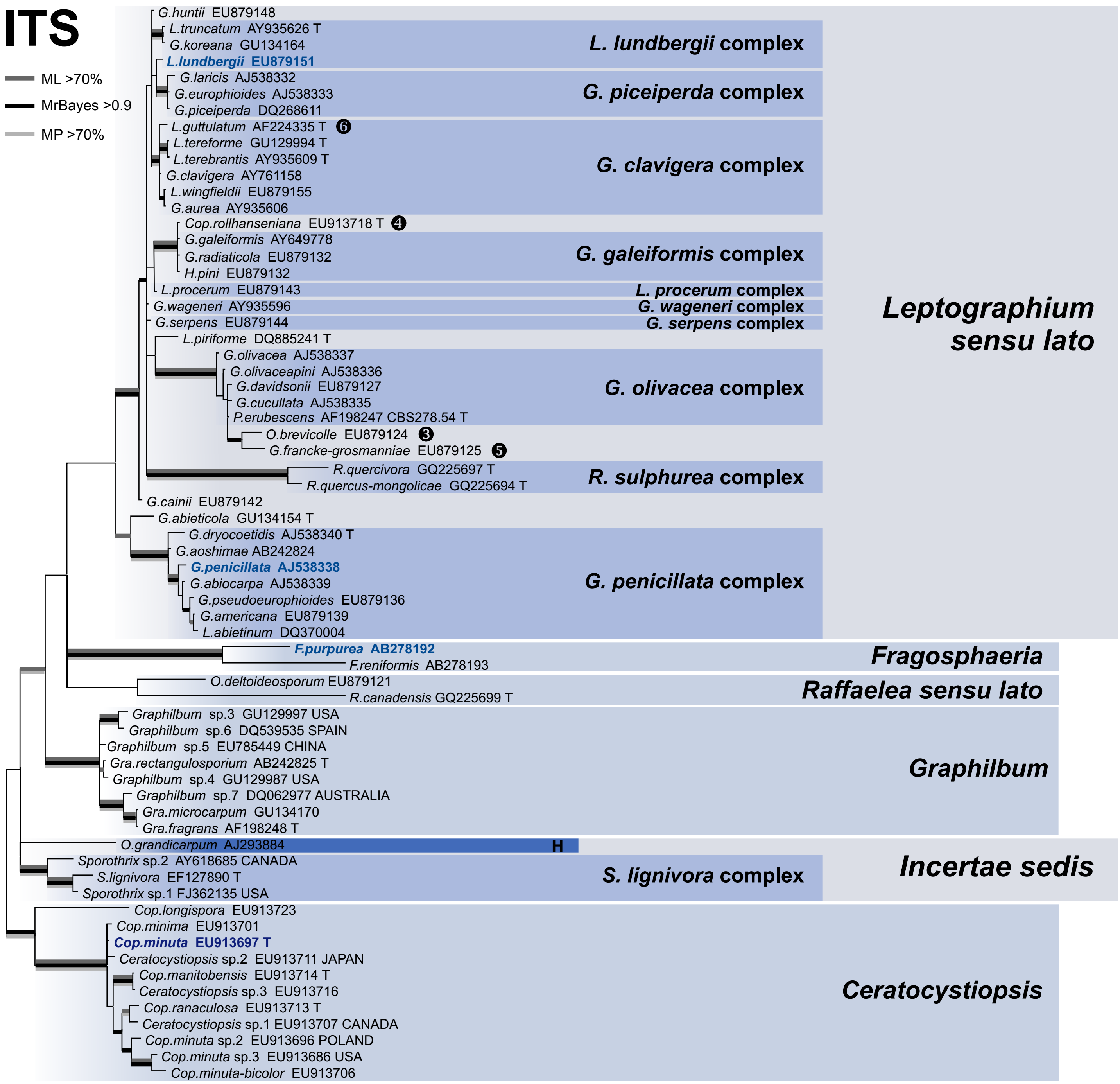
Figs 4a, b Phylogram obtained from Bayesian Inference resulting from the analyses of the LSU sequences of 216 species of the *Ophiostomatales*. Genera and species complexes are delineated by shaded blocks. Blocks marked alphabetically indicate lineages not forming part of the major groups, lacking statistical support, or represented by only one or two taxa. Species with conflicting generic placement are indicated by numbers in black circles. Type species of currently accepted genera are printed in blue type in boxes. Genera currently treated as synonyms are printed in parentheses next to their type species.


LSU
Raffaelea s. str.
Ophiostoma s. str.
Ophiostoma s. l.
Ceratocystiopsis
Fragosphaeria
Leptographium s. l.
Graphilbum
O.seticolle AF135578 ❶
O.deltoideosporum Hausner 1993
R.tritirachium EU177464 T
R.albimanens EU177452 T
R.sulcati EU177462 T
R.santoroi EU984302
R.subalba EU177443 T
Raffaelea sp.1 EU177467 SOUTH AFRICA
Raffaelea sp.2 EU177466 USA
Raffaelea sp.3 EU177465 USA
R.canadensis EU177458 T
R.subfusca EU177450 T
R.fusca EU177449 T
R.ellipticospora EU177446 T
R.ambrosiae EU177453 T
R.scolytodis AM267270
R.gnathotrichi EU177460 T
R.arxii EU177454 T
Raffaelea sensu stricto
O.microsporum CMW17152 T
A
O.ulmi DQ294374 (Pesotum)
O.novo-ulmi DQ294375
O.torulosum AF155683
O.quercus DQ294376
O.australiae EF408608
O.catonianum AF136950
O.karelicum EU443756
O.triangulosporum AF135581
O. ulmi complex
O.tetropii CBS428.94
O.araucariae DQ294373
O.piceae AF234837
O.setosum AF128929
O.brunneum AF135580
O.canum DQ294372 (Pachnodium)
O.flexuosum DQ294370
O.distortum DQ294369
O.carpenteri DQ294363
O.retusum L05783
O.longirostellatum AF155688
O.conicolum AF155689
O.subannulatum DQ294364
O.pluriannulatum DQ294365
O.californicum AF137280
O.longiconidiatum CMW17574
O.populinum Hausner 1993
O.multiannulatum DQ294366
O. pluriannulatum complex
O.introcitrinum Hausner 1993 (Hyalopesotum)
O.minus Hausner 1993 North America
O.pseudominus Hausner 1993
O.minus AM943887 Europe
Ophiostoma sensu stricto
O.piliferum DQ294377
O.floccosum AF234836
O.brunneo-ciliatum AF135576
O.ainoae DQ294368
O.macrosporum AF282873
O.tingens AF282871
Ophiostoma sp.1 AF282869 NORWAY
Ophiostoma sp.2 EU984282 NORWAY
B
O.japonicum GU134184 T
O.trinacriforme AF155687 CFB527 ❷
O.tremulo-aureum AF135573
H.ips AF282872
O.montium DQ294379
O.ips DQ294381
O.columnare Hausner 1993
O.bicolor Hausner 1993
O.adjuncti AF155686
O.pulvinisporum DQ294380
Ophiostoma sp.3 GU221906 USA
O.hyalothecium AF137284
O. ips complex
L.brachiatum AF343676
L.antibioticum AF343677
C
O.pseudonigrum AF135577
O.grande CMW1036 T
O.ambrosium AF137285
D
O.fasciatum EU913680
O.crenulatum AF135589
E
R.lauricola EU177440 T
R.brunnea EU177457
Raffaelea sp.4 EU984281 CANADA
R. lauricola complex
O.nigricarpum DQ294356
O. tenellum complex
O.gemellus DQ821531 T
O.abietinum AF155685
O.palmiculminatum DQ316143
S.humicola EF139114
O.protearum DQ316145
O.africanum DQ316147
O.brevicolle AF343678 ❸
O.bragantinum CMW17149 T
O.fusiforme DQ294354
O.gossypinum AF137282
O.lunatum DQ294355
O.narcissi AF135572
O.phasma DQ316151
O.trinacriforme AF343671 CMW670 ❷
O.stenoceras DQ836904
O.splendens AF221013
S.inflata DQ294351
S.pallida EF139121
S.schenckii DQ294352 (Sporothrix)
S.stylites EF139115
S.variecibatus DQ821537
S. schenckii-O. stenoceras complex
Ophiostoma sensu lato
Cop.ranaculosa DQ294357
Cop.brevicomis EU913683 T
Ceratocystiopsis sp.3 EU913676 CANADA
Ceratocystiopsis sp.1 EU913667 CANADA
Cop.collifera EU913681 T
Cop.manitobensis DQ294358
Cop.minuta-bicolor DQ294359 (Hyalorhinocladiella)
Cop.minuta sp.3 EU913645 USA
Cop.rollhanseniana DQ294362 ❹
Cop.minuta sp.2 EU913655 POLAND
Cop.minuta EU913656 T
Cop.concentrica AF135571
Ceratocystiopsis sp.2 EU913671 JAPAN
Cop.parva L05805
Cop.minima DQ294361
Cop.neglecta CBS100596 T
Cop.pallidobrunnea EU913682
Cop.longispora EU913684
Ceratocystiopsis
ML >70%
MrBayes >0.9
MP >70%
0.2


LSU
Raffaelea s. str.
Ophiostoma s. str.
Ophiostoma s. l.
Ceratocystiopsis
Fragosphaeria
Leptographium s. l.
Graphilbum
F.reniformis AB189155
F.purpurea AF096191
Fragosphaeria
L.truncatum DQ062052
L.lundbergii DQ294388
G.koreana AY707197 T
L.conjunctum HQ406831 T
L.pinicolum DQ062060 T
G.yunnanensis AY707207
L. lundbergii complex
G.huntii DQ294387
G.clavigera GENOME (Graphiocladiella)
G.aurea DQ294389
L.wingfieldii AY553398 T
L.pyrinum DQ062072 T
G.robusta AY553397 T
L.longiclavatum AY816686 T
L.terebrantis EU296777 T
G. clavigera complex
L.manifestum HQ406839 T
L.celere HQ406834 T
L.sinoprocerum EU296773 T
L.profanum DQ354944 T
L.procerum AY553386
L.latens HQ406845 T
L.gracile HQ406840 T
L.pinidensiflorae DQ062082
L.bhutanense EU650187 T
L. procerum complex
O.brevicolle AF155670 ❸
G.francke-grosmanniae AF155669 ATCC22061 T ❺
L.albopini AF343695
G.radiaticola AY744551 T
G.galeiformis DQ294383
G. galeiformis complex
G.olivaceapini AJ538336
G.cucullata AJ538335
G.davidsonii GU134165-GU134181
G.olivacea AJ538337
G.sagmatospora AY744546 (Phialographium)
G.vesca AF155671
G. olivacea complex
G.leptographioides DQ294382
L.piriforme FM992031
G.crassivaginata DQ294386
G.europhioides AJ538333
G.aenigmatica DQ294391
G.laricis DQ294393
G.piceiperda DQ294392
G. piceiperda complex
L.neomexicanum AY553382
G.wageneri DQ294396
L.reconditum AY553383
L.wageneri var. pseudotsugae AF343706
L.douglasii AY553380
L.wageneri var. wageneri AF343707
G. wageneri complex
Leptographium sensu lato
G.francke-grosmanniae DQ294395 CMW2975 ❺
G.cainii AY744548
G.serpens JN135314 T
G.alacris JN135313 T
L.castellatum JN135317 T
L.gibbsii JN135316 T
L.yamaokae JN135315 T
G. serpens complex
L.pineti DQ062076
L.pruni AB091219-AB104900
L.alethinum EU502800
G.grandifoliae DQ294399
L.pityophilum AF343679
R.quercivora AB496454 T
R.montetyi EU984301
R.sulphurea EU177463 T
R.amasae EU984295 (Dryadomyces)
R. sulphurea complex
L.elegans AF343675
Esteya vermicola EU627684 (Esteya)
F
L.taigensis JF280017 T
G.abieticola GU134177 T
L.verrucosum CMW17160 T
L.guttulatum AF343683 T ❻
L.euphyes AF343686
L.curvisporum EU979328 T
L.curviconidium HQ406850 T
L.chlamydatum EU979333 T
L.altius HQ406851 T
L.abietinum EU177472
G.pseudoeurophioides AF155678
G.penicillata DQ294385 (Grosmannia)
G.americana DQ062078
G.abiocarpa AJ538339
G.aoshimae AB235156
G.dryocoetis AJ538340 T
L.fruticetum DQ097849
L.pistaciae HQ406846 T
L.hughesii AF343700
L.eucalyptophilum AF343703
L.bistatum AY348304
L.abieticolens AF343701 T
G.francke-grosmanniae AF343702 CMW445 T ❺
G. penicillata complex
S.lignivora EF139119 T
S. lignivora complex
Incertae sedis
Graphilbum sp.2 AY672929 CANADA
Gra.rectangulosporium AB235158 T
Gra.nigrum AF137281 T
Gra.curvicolle AF135585 T
Gra.sparsum AF135575 T
Graphilbum sp.3 GU221905 USA
Gra.microcarpum GU134186
Gra.fragrans CMW19357
Graphilbum
Podospora decipiens AY780073
Sordaria fimicola AY545728
Neurospora crassa AF286411
ML >70%
MrBayes >0.9
MP >70%
0.2

Figs 5a, b Phylograms resulting from ML analyses of the ITS sequences of 156 species of the *Ophiostomatales*, divided in two data sets. Genera and species complexes are delineated by shaded blocksBlocks marked alphabetically indicate lineages not forming part of the major groups, lacking statistical support, or represented by only one or two taxa. Species with conflicting generic placement are indicated by numbers in black circles.


ITS
ML >70%
MrBayes >0.9
MP >70%
O.tasmaniense GU797211 T
O.catonianum AF198243 T
O.borealis EF408593 T
O.australiae EF408603 T
O.denticiliatum FJ804490 T
O.quercus AY466626 T
O.undulatum GU797218 T
O.tsotsi FJ441287 T
O.bacillisporum AY573258
O.novo-ulmi subsp. americana AF198236
O.novo-ulmi subsp. novo-ulmi AF198235
O.himalulmi AF198233
O.ulmi AF198232
O.karelicum EU443762 T
O.triangulosporum AY934525 T
O. ulmi complex
O.tetropii AY934524
O.brunneociliatum HM031500
O.ainoae HM031495
O.tapionis HM031493 T
O.floccosum AF198231 T
O.piceae AF198226 T
O.setosum AF128929 T
O.breviusculum AB200423 T
O.canum HM031489 T
O.flexuosum AY924387 T
O.rachisporum HM031490 T
O.cupulatum AF198230 T
O.distortum AY924386 T
O.arduennense AY573241 T
O.subalpinum AB096211
O.ssiori AB096209 T
O.nikkoense AB506674
O.kryptum AY304436 T
O.allantosporum AY934506
O.minus HM031497 RUSSIA
O.minus AY934511 SPAIN
O.minus AF234834 CANADA
O.piliferum AF221070
O.pseudotsugae AY542502
Ophiostoma sensu stricto
O.longiconidiatum EF408558 T
O.conicolum AY924384 T
O.multiannulatum AY934512 T
O.subannulatum AY934522 T
O.sparsiannulatum CMW17231 T
O.pluriannulatum AY934517
O. pluriannulatum complex
O.japonicum GU134169 T
Ophiostoma sp. 4 GU129996 USA
O.montium AY546711
O.bicolor DQ268604 T
O.fuscum HM031504 T
O.adjuncti AY546696 T
O.ips AY546704 T
O.pulvinisporum AY546714 T
O. ips complex
O.bragantinum FN546965 T
O.candidum HM051409 T
S.stylites EF127883 T
S.pallida EF127880 T
S.humicola AF484472 T
O.proteasedis EU660449 T
O.palmiculminatum DQ316191 T
O.gemellus DQ821560 T
S.dimorphospora AY495428 T
S.inflata AY495426 T
O.dentifundum AY495434 T
O.phasma DQ316219 T
S.schenckii AY280495
S.luriei AB128012 T
S. schenckii-O. stenoceras complex
O.zambiensis EU660453 T
O.splendens DQ316205
O.protearum DQ316203
O.africanum DQ316200
O.fusiforme AY280481 T
O.lunatum AY280485 T
O.abietinum AF484453 T
O.aurorae DQ396796 T
S.variecibatus DQ821568 T
O.stenoceras AF484462 T
O.seticolle AF194511 T ❶
O.rostrocoronatum AY194509
O.narcissi AF194510 T
Ophiostoma sensu lato
O.coronatum AY924385
O.tenellum AY934523
O.nigricarpum AY280489 T
O. tenellum complex
O.saponiodorum HM031507 T
O.pallidulum HM031510 T
F
O.sejunctum AY934519 T
O.angusticollis AY924383
G
O.fumeum HM051412 T
S.brunneoviolaceae FN546959 T
O.fasciatum EU913720
E
0.05


ITS
ML >70%
MrBayes >0.9
MP >70%
G.huntii EU879148
L.truncatum AY935626 T
G.koreana GU134164
L.lundbergii EU879151
L. lundbergii complex
G.laricis AJ538332
G.europhioides AJ538333
G.piceiperda DQ268611
G. piceiperda complex
L.guttulatum AF224335 T ❻
L.tereforme GU129994 T
L.terebrantis AY935609 T
G.clavigera AY761158
L.wingfieldii EU879155
G.aurea AY935606
G. clavigera complex
Cop.rollhanseniana EU913718 T ❹
G.galeiformis AY649778
G.radiaticola EU879132
H.pini EU879132
G. galeiformis complex
L.procerum EU879143
L. procerum complex
G.wageneri AY935596
G. wageneri complex
G.serpens EU879144
G. serpens complex
Leptographium sensu lato
L.piriforme DQ885241 T
G.olivacea AJ538337
G.olivaceapini AJ538336
G.davidsonii EU879127
G.cucullata AJ538335
P.erubescens AF198247 CBS278.54 T
G. olivacea complex
O.brevicolle EU879124 ❸
G.francke-grosmanniae EU879125 ❺
R.quercivora GQ225697 T
R.quercus-mongolicae GQ225694 T
R. sulphurea complex
G.cainii EU879142
G.abieticola GU134154 T
G.dryocoetidis AJ538340 T
G.aoshimae AB242824
G.penicillata AJ538338
G.abiocarpa AJ538339
G.pseudoeurophioides EU879136
G.americana EU879139
L.abietinum DQ370004
G. penicillata complex
F.purpurea AB278192
F.reniformis AB278193
Fragosphaeria
O.deltoideosporum EU879121
R.canadensis GQ225699 T
Raffaelea sensu lato
Graphilbum sp.3 GU129997 USA
Graphilbum sp.6 DQ539535 SPAIN
Graphilbum sp.5 EU785449 CHINA
Gra.rectangulosporium AB242825 T
Graphilbum sp.4 GU129987 USA
Graphilbum sp.7 DQ062977 AUSTRALIA
Gra.microcarpum GU134170
Gra.fragrans AF198248 T
Graphilbum
O.grandicarpum AJ293884
H
Sporothrix sp.2 AY618685 CANADA
S.lignivora EF127890 T
Sporothrix sp.1 FJ362135 USA
S. lignivora complex
Incertae sedis
Cop.longispora EU913723
Cop.minima EU913701
Cop.minuta EU913697 T
Ceratocystiopsis sp.2 EU913711 JAPAN
Cop.manitobensis EU913714 T
Ceratocystiopsis sp.3 EU913716
Cop.ranaculosa EU913713 T
Ceratocystiopsis sp.1 EU913707 CANADA
Cop.minuta sp.2 EU913696 POLAND
Cop.minuta sp.3 EU913686 USA
Cop.minuta-bicolor EU913706
Ceratocystiopsis

Chapter 3

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A nomenclator for ophiostomatoid genera and species in the *Ophiostomatales* and *Microascales*

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Abstract

In this updated nomenclator, the names of 596 species proposed for ophiostomatoid fungi are considered. The result is 371 accepted species in 12 genera classified in the *Ophiostomatales* and *Microascales*. The taxonomic status of each species was re-evaluated based on all published details and where available, phylogenetic inferences, and data on typification. The principle of single name nomenclature, as adopted by the 18th International Botanical Congress, Melbourne in July 2011, was applied to all genera and species. Based on these re-assessments, three genera were redefined: *Graphilbum* in the *Ophiostomatales*, and *Graphium* and *Knoxdaviesia* (=*Gondwanamyces*) in the *Microascales*. Species were reclassified as necessary, resulting in 28 new combinations and one new name. *Ophiostoma s.l.* now includes 134 accepted species, *Ceratocystiopsis* 16 species, *Fragosphaeria* two, *Graphilbum* eight, *Raffaelea s.str.* 13, and *Leptographium s.l.* (including *Grosmannia*) 93. A further 29 species could not be assigned to any of these six genera with certainty, and seven more species were invalidly described. In the *Microascales*, *Ceratocystis* contains 72 accepted species, *Graphium* nine, *Knoxdaviesia* nine, and *Sphaeronaemella* seven, while *Cornuvesica* and *Custingophora* are both monotypic. Twenty microascalean species of uncertain status and six invalidly published species remain. Type studies and evaluation of the literature allowed the remaining 167 species described in the classical concept of *Graphium* to be reconsidered. Finally, 19 species previously assigned to *Ceratocystis*, *Ceratostomella*, *Leptographium*, *Ophiostoma*, *Raffaelea*, *Sphaeronaemella* and/or *Sporothrix*, were excluded from both the *Ophiostomatales* and *Microascales*.

Taxonomic novelties:

Cephalotrichum album (Costantin) Seifert, *comb. nov.*, *Ceratocystiopsis neglecta* (Kirschner & Oberw.) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Ceratocystis harringtonii* Z.W. de Beer & M.J. Wingf. *nom. nov.*, *Graphilbum brunneocrinitum* (E.F. Wright & Cain) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Graphilbum curvicolle* (Olchow. & J. Reid) Z.W. de Beer & M.J. Wingf. , *comb. nov.*, *Graphilbum fragrans* (Math.-Käärik) Z.W. de Beer, Seifert & M.J. Wingf. , *comb. nov.*, *Graphilbum microcarpum* (Yamaoka & Masuya), Z.W. de Beer, & M.J. Wingf., *comb. nov.*, *Graphilbum nigrum* (R.W. Davidson), Z.W. de Beer & M.J. Wingf. , *comb. nov.*, *Graphilbum rectangulosporium* (R.W. Davidson), Z.W. de Beer, & M.J. Wingf., *comb. nov.*, *Graphilbum tubicolle* (Olchow. & J. Reid) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Grosmannia truncicola* (R.W. Davidson) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Knoxdaviesia cecropiae* (M. Kolařík) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Knoxdaviesia scolytodis* (M. Kolařík) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Knoxdaviesia serotectus* (Van der Linde & Jol. Roux) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Knoxdaviesia suidafrikana* (Morgan-Jones & R.C. Sinclair) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Knoxdaviesia ubusi* (Van der Linde & Jol. Roux) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Knoxdaviesia undulatistipes* (Pinnoi) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Knoxdaviesia wingfieldii* (Roets & Dreyer), Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Leptographium obscurum* (R.W. Davidson) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Leptographium rostrocylindricum* (R.W. Davidson) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Leptographium verrucosum* (Gebhardt, R. Kirschner & Oberw.) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Ophiostoma australiae*

(Kamgan, K. Jacobs & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Ophiostoma cupulatum* (McNew & Harrington) Z.W. de Beer & M.J. Wingf. , *comb. nov.*, *Ophiostoma denticulatum* (R.W. Davidson) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Ophiostoma leucocarpum* (R.W. Davidson) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Ophiostoma macrosporum* (Francke-Grosm.) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Ophiostoma populicola* (Olchow. & J. Reid) Z.W. de Beer, Seifert, M.J. Wingf. *comb. nov.*, *Ophiostoma tingens* (Lagerb. & Melin) Z.W. de Beer & M.J. Wingf. *comb. nov.*, *Phaeostilbella nigrum* (Berk.) Seifert, *comb. nov., Sphaeronaemella betae* (Delacr.) Z.W. de Beer & M.J. Wingf. *comb. nov., Stilbocrea aterrima* (Welw. & Curr.) Seifert, *comb. nov.*

INTRODUCTION

Presented here is a nomenclatural implementation of the taxonomic concepts for ophiostomatoid fungi proposed elsewhere in this volume by De Beer *et al*. (2012), De Beer & Wingfield (2012) and B. Wingfield *et al*. (2012). The nomenclator includes all genera and species currently classified in the *Ophiostomataceae* (*Ophiostomatales*), *Ceratocystidaceae*, *Gondwanamycetaceae* and *Graphiaceae* (*Microascales*). In this listing, we follow the single name principle accepted at the 18th International Botanical Congress held in Melbourne during July 2011 (Hawksworth 2011, Hawksworth *et al*. 2011, Norvell 2011). These principles are being incorporated into the newly named International Code of Nomenclature for Algae, Fungi and Plants (ICN) and will enforce equal status for taxa (i.e. genera and species) whether they were originally described as either teleomorphic or anamorphic. To maintain nomenclatural stability and avoid premature and unnecessary name changes, we followed recommendations explained by De Beer *et al*. (2012), De Beer & Wingfield (2012) and B. Wingfield *et al*. (2012).

Genera

In the nomenclator, we apply the generic concepts defined by De Beer & Wingfield (2012) for the *Ophiostomatales*, and include all genera in that order. Not all fungi in the *Microascales* are considered ophiostomatoid (De Beer *et al.* 2012). Therefore, we only consider genera of the three ophiostomatoid families in that order, the *Ceratocystidaceae*, *Gondwanamycetaceae* and *Graphiaceae*. For the *Microascales*, we apply generic concepts as defined by B. Wingfield *et al.* (2012) and De Beer *et al.* (2012). *Sphaeronaemella* could not be placed with confidence in a microascalean family (De Beer *et al.* 2012), but we included it in our list because several of its species were previously classified in *Ceratocystis*, and were thus considered ophiostomatoid.

In cases where a currently accepted genus includes the type species of different genera, priority is given to the genus name that was described first. All other genus names are treated as its synonyms, irrespective of the morph they previously represented.

Species

All species are listed under the genus in which they are currently treated in the accompanying papers by De Beer & Wingfield (2012) and B. Wingfield *et al.* (2012); this nomenclature has been applied throughout this book. Three genera, *Ophiostoma sensu lato* (*s.l.*), *Leptographium s.l.*, and *Ceratocystis s.l.,* include species with generic names differing from the genus where they are listed. This reflects the taxonomic uncertainties surrounding these species, usually the consequence of inadequate phylogenetic support and the need for additional multi-gene studies or more intensive sampling. For example, *Leptographium antibioticum* is not part of *Leptographium s.l.*, but of *Ophiostoma s.l.* based on rDNA phylogenies (De Beer & Wingfield 2012), and is presently listed under the latter genus until its accurate phylogenetic classification can be assured. To improve searchability within these *sensu lato* genera, the species are alphabetically ordered by epithet, rather than their current genus name.

Under the dual nomenclature system, previous monographs and nomenclators distinguished between teleomorph and anamorph binomials. These names now have equal status and we thus treat all names applied to any single species as equal synonyms. These synonyms are listed under the relevant species in order of priority; we have indicated those that were originally considered anamorphs names in the synonymies.

Sections

The nomenclator is subdivided as follows:

A. The *Ophiostomatales*
  1. Accepted genera and species
  2. Valid species of uncertain status
  3. Invalidly published species.

B. The ophiostomatoid genera and species in the *Microascales*
  1. Accepted genera and species
  2. Valid species of uncertain status
  3. Invalidly published species.

C. Species excluded from the ophiostomatoid genera in the *Ophiostomatales* and *Microascales*
  1. Species described in *Graphium.*
  2. Species described in other genera.

How to read the nomenclator

Currently accepted name (Original author/s) Author/s of new combination, Journal Vol: page number of species description or new combination. Year. MYCOBANK number for new names ≡ Homotypic synonyms (i.e. synonyms based on the same type specimen) (basionyms are indicated when the accepted name is the result of a new combination in this paper) = Heterotypic synonyms (i.e. synonyms based on different types) [square brackets include original, incorrect spelling of epithet if it has been corrected (Art. 23.5, 32.7, 60.1, 60.11), OR it contains an indication whether a name was invalidly or illegitimately described, together with the relevant article of the Vienna Code (McNeill *et al.* 2006),(see Text Box 1)].

Anamorph: In accordance with single name nomenclature, separate generic names should no longer be used to classify anamorphs. The format for our designation of anamorphs is as suggested by Cannon & Kirk (2000), as endorsed by Hawksworth (2011). When a species makes two or more morphologically distinct anamorphs, they are referred to as synanamorphs and then that is used as the heading for the paragraph.

Descriptions: References to detailed morphological descriptions and/or illustrations of the species. If the only description is the protologue, this paragraph is not included.

Phylogenetic data: References where DNA sequence data for this species and/or its synonyms were used in phylogenetic analyses. If no phylogenetic data presently exists, we have not included a paragraph with this heading.

Notes: Additional information, in most cases explaining synonymies and/or uncertainties surrounding the status of species, and the current placement of a species in a species complex based on phylogenetic analyses.

A.1. ACCEPTED GENERA AND SPECIES IN THE *OPHIOSTOMATALES*

Genus concepts as defined by De Beer & Wingfield (2012) are applied here. Under *Ophiostoma* and *Leptographium*, we list all species treated respectively in *Ophiostoma s.l.* and *Leptographium s.l.* as defined by De Beer & Wingfield (2012), following their recommendations to ensure nomenclatural stability under the emended Code.

Ophiostoma Syd., *In* Sydow & Sydow, Annls mycol. 17: 43. 1919 [type species *O. piliferum*]
?= *Sporothrix* Hektoen & C.F. Perkins, J. Exp. Med. 5: 80. 1900. Anamorphic synonym. [type species *S. schenckii*]

= *Sporothrix* section *Sporothrix* Weijman & de Hoog, Antonie van Leeuwenhoek 51: 118. 1985.
= *Sporotrichopsis* Gueguen, *In* De Beurmann & Gougerot, Archs Parasit. 15: 104. 1911. Anamorphic synonym. [type species *S. beurmannii*; *nom. inval*., Art. 34.1]
= *Dolichoascus* Thibaut & Ansel, *In* Ansel & Thibaut, Compt. Rend. Hebd. Séances Acad. Sci. 270: 2173. 1970. Teleomorphic synonym. [type species *D. schenckii*; *nom. inval*., Art. 37.1]
= *Linostoma* Höhn., Annls mycol. 16: 91. 1918 [*nom. illegit*., Art. 53.1, see De Beer *et al.* 2012].
= *Ophiostoma* Syd. section *Longirostrata* Nannf. *pro parte*, *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 407. 1934.
= *Ophiostoma* Syd. section *Brevirostrata* Nannf., *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 407. 1934.
?= *Europhium* A.K. Parker, Can. J. Bot. 35: 175. 1957. Teleomorphic synonym. [type species *O. trinacriforme*]
= *Pesotum* J.L. Crane & Schokn., Am. J. Bot. 60: 347. 1973. Anamorphic synonym. [type species *P. ulmi* (M.B. Schwarz) J.L. Crane & Schokn. 1973]
= *Hyalopesotum* H.P. Upadhyay & W.B. Kendr., Mycologia 67: 801. 1975. Anamorphic synonym. [type species *H. introcitrinum* H.P. Upadhyay & W.B. Kendr. 1975]
= *Pachnodium* H.P. Upadhyay & W.B. Kendr., Mycologia 67: 802. 1975. Anamorphic synonym. [type species *P.canum* H.P. Upadhyay & W.B. Kendr. 1975]
= *Ceratocystis* Ellis & Halst. section *Ophiostoma* (Syd.) H.P. Upadhyay *pro parte*, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 85. 1981 [type species *O. piliferum*]
= *Ceratocystis* Ellis & Halst. section *Ips* H.P. Upadhyay *pro parte*, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 70. 1981 [type species *O. ips*]

Note: In the majority of papers, the authority for *Ophiostoma* is given as Syd. & Syd., or in some cases H. & P. Sydow. Although the original publication had two authors, the authority of the genus name and new combinations in the paper were explicitly attributed only to Sydow (p. 43, Sydow & Sydow 1919). Von Arx (1952) and von Arx & Müller (1954) were the only authors to date to correctly follow the Code (Art. 46.2) by using only ‘Syd.’

The genus *Sporothrix* was initially described without a generic diagnosis (Hektoen & Perkins 1900), which prompted Nicot & Mariat (1973) to provide a Latin diagnosis to validate the name. de Hoog (1974) accepted the emended description of Nicot & Mariat (1973). However, Domsch *et al.* (1980) regarded the validation unnecessary ‘in view of the rather exhaustive *descriptio generico-specifica* (Art. 42)’ by Hektoen & Perkins (1900). Under the Melbourne Code, *Sporothrix*, as the older name will have priority over *Ophiostoma*, which imply that the latter should be treated as synonym of *Sporothrix*. However, De Beer & Wingfield (2012) showed that the *S. schenckii-O. stenoceras* complex forms a lineage distinct from *Ophiostoma. s.str*., which might represent a distinct genus. For the present they suggested that the complex be treated as part of *Ophiostoma s.l.* The synonymies of *Sporotrichopsis* and *Dolichoascus* with *Sporothrix* are discussed under *S. schenckii*.

The uncertain generic status of *Europhium* is a result of the uncertain placement of its type species, *O. trinacriforme* (see section A.2, and De Beer & Wingfield, 2012).

The type species for *Pesotum*, *Hyalopesotum* and *Pachnodium* all group in *Ophiostoma s.str.* (De Beer & Wingfield, 2012), rendering these genera synonyms of *Ophiostoma* under the Melbourne Code.

Upadhyay (1981) designated official sections in *Ceratocystis*. Apart from two *Sphaeronaemella* spp., all the taxa he included in his Section *Ophiostoma* are at present included in *Ophiostoma s.l.* Similarly, most species in his Section *Ips* are included in *Ophiostoma s.l.*, with four of the species included in *Graphilbum.*

The fungal genus *Ophiostoma* should not be confused with *Ophiostoma* Rudolphi, a genus of parasitic nematodes (Table 1; De Beer *et al.* 2012).

Ophiostoma abietinum Marm. & Butin, Sydowia 42: 194. 1990.

Anamorph: sporothrix-like.

Description: Marmolejo & Butin (1993, pp 157, 166, Figs 1–4).

Phylogenetic data: Hausner *et al.* (1993b, 2000); De Beer *et al.* (2003d); Aghayeva *et al.* (2004); Masuya *et al.* (2004); Zhou *et al.* (2004b, 2006); Villarreal *et al.* (2005); Roets *et al*. (2008, 2010); Lu *et al.* (2009a); Massoumi Alamouti *et al.* (2009); Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Notes: De Beer *et al.* (2003d) erroniously treated several isolates, including the ex-type of *O. abietinum*, as the *'O. nigrocarpum* complex*'*. Aghayeva *et al.* (2004) showed that the ex-type strains of *O. nigricarpum* and *O. abietinum* are distinct, and that De Beer's isolates grouped with the latter species. *Ophiostoma abietinum* belongs to the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012). The name should not be confused with *L. abietinum* (listed under *Leptographium*), which is a different fungus and a coincidental epithet.

Ophiostoma adjuncti (R.W. Davidson) Harrington, Mycotaxon 28: 41. 1987 ≡ *Ceratocystis adjuncti* R.W. Davidson, Mycologia 70: 35. 1978.

Anamorph: hyalorhinocladiella- to pesotum-like.

Description: Upadhyay (1981, p. 79).

Phylogenetic data: Hausner *et al.* (1993b; 2000); Masuya *et al.* (2004); Zhou *et al.* (2004b); Lu *et al.* (2009a); Linnakoski *et al.* (2010).

Notes: Considered a synonym of *O. ips* by Upadhyay (1981) and Hutchison & Reid (1988a), but as distinct from *O. ips* by Harrington (1987, 1988), Hausner *et al.* (1993b, 2000), and Zhou *et al.* (2004b). This fungus belongs to the *O. ips* species complex based on rDNA phylogenies (De Beer & Wingfield 2012).

Ophiostoma africanum G.J. Marais & M.J. Wingf., Mycol. Res. 105: 241. 2001 = *Sporothrix africanum* G.J. Marais & M.J. Wingf., Mycol. Res. 105: 242. 2001.

Anamorph: sporothrix-like.

Phylogenetic data: Viljoen *et al.* (1999); Wingfield *et al.* (1999); Roets *et al.* (2006, 2008, 2010, 2012); Zipfel *et al.* (2006); De Meyer *et al*. (2008); Harrington *et al.* (2010); De Beer & Wingfield (2012).

Notes: Forms part of the *S. schenckii – O. stenoceras* species complex (De Beer & Wingfield 2012).

Ophiostoma ainoae H. Solheim, Nord. J. Bot. 6: 201. 1986.

Anamorph: pesotum-like.

Description: Yamaoka *et al.* (1997, pp 1219–1220).

Phylogenetic data: Okada *et al.* (1998); Hausner & Reid (2003); Gebhardt *et al.* (2005)*;* Zipfel *et al.* (2006); Linnakoski *et al.* (2008, 2010); De Beer & Wingfield (2012).

Notes: Authentic isolates of *O. ainoae* from Norway were peripheral to *O. piceae* and its sibling species (Hausner & Reid 2003, Zipfel *et al.* 2006), and were treated in the *'O. ips sensu lato*' complex by Linnakoski *et al.* (2010). In the analyses of De Beer & Wingfield (2012), the species groups with *O. brunneo-ciliatum* and *O. tapionis*, closer to *O. floccosum* in *Ophiostoma s.str*. One Japanese isolate (JCM 9356) identified as *O. ainoae* and grouping with *G. cucullata*, *G. europhioides* and *G. penicillata* (Okada *et al.* 1998; Gebhardt *et al.* 2005), is probably an undescribed species.

Ophiostoma allantosporum (Griffin) M. Villarreal, Mycotaxon 92: 262. 2005 ≡ *Ceratocystis allantospora* H.D. Griffin, Can. J. Bot. 46: 694. 1968.

Anamorph: hyalorhinocladiella-like.

Descriptions: Olchowecki & Reid (1974, p. 1704, Pl. XVI Fig. 315); Upadhyay (1981, p. 88). Figure number cited in the description of *C. allantospora* by Upadhyay (1981) actually refer to those in the protologue, not his monograph.

Phylogenetic data: Villarreal *et al.* (2005); Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Notes: The species is closely related to *O. kryptum* and *O. minus* (De Beer & Wingfield 2012; Linnakoski *et al*. 2010).

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

Anamorph: raffaelea-like.

Description: Hunt (1956, p. 44).

Phylogenetic data: Hausner *et al.* (1993b); Hausner & Reid (2003); De Beer & Wingfield (2012).

Notes: Griffin (1968), Upadhyay (1981), Hutchison & Reid (1988a) and Seifert *et al.* (1993) listed *O. ambrosium* as synonym of *O. piliferum*, but Hunt (1956) and de Hoog (1974) treated it as distinct. De Beer & Wingfield (2012) showed that the short LSU sequence from Hausner *et al.* (1993b) groups in a distinct lineage with *O. grande* in *Ophiostoma s.l.*

Leptographium antibioticum (W.B. Kendr.) M.J. Wingf., Trans. Br. Mycol. Soc. 85: 92. 1985 ≡ *Verticicladiella antibiotica* W.B. Kendr., Can. J. Bot. 40: 789. 1962.

Anamorph: leptographium-like.

Descriptions: Kendrick (1962, pp 789–793, Figs 7, 10A–D); Jacobs & Wingfield (2001, pp 64–66, Figs 37–39).

Phylogenetic data: Jacobs *et al.* (2001d); Masuya *et al.* (2004); Massoumi Alamouti *et al.* (2006); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); De Beer & Wingfield (2012).

Notes: De Beer & Wingfield (2012) showed that this species is in a clade with *L. brachiatum* in *Ophiostoma s.l.,* and not in *Leptographium* as suggested by Jacobs *et al.* (2001d).

Ophiostoma angusticollis (Wright & Griffin) M. Villarreal, Mycotaxon 92: 262. 2005 ≡ *Ceratocystis angusticollis* Wright & H.D. Griffin, *In* Griffin, Can. J. Bot. 46: 697. 1968.

Anamorph: sporothrix-like.

Descriptions: Olchowecki & Reid (1974, p. 1704, Pl. XV Figs 296–302); Upadhyay (1981, p. 89, Figs 303–307).

Phylogenetic data: Villarreal *et al.* (2005); De Beer & Wingfield (2012).

Notes: Villarreal *et al.* (2005) and De Beer & Wingfield (2012) showed that *O. angusticollis* groups with *O. sejunctum* close to, but distinct from, the *O. tenellum* complex.

Ophiostoma araucariae (Butin) de Hoog & Scheffer, Mycologia 76: 297. 1984 ≡ *Ceratocystis araucariae* Butin, Can. J. Bot. 46: 61. 1968.

Anamorph: pesotum-like.

Descriptions: Olchowecki & Reid (1974, p. 1709); Upadhyay (1981, p. 90, Figs 308–313); de Hoog & Scheffer (1984, pp 293–295, Fig. 1).

Phylogenetic data: Hausner *et al.* (1993b); Gebhardt *et al.* (2004, 2005); Zipfel *et al.* (2006); Linnakoski *et al.* (2008); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species groups in *Ophiostoma s. str.* (De Beer & Wingfield 2012).

Ophiostoma arborea (Olchow. & J. Reid) Yamaoka & M.J. Wingf., *In* Yamaoka *et al.*, Mycol. Res. 101: 1223. 1997 ≡ *Ceratocystis arborea* Olchow. & J. Reid, Can. J. Bot. 52: 1688. 1974.

Anamorph: pesotum-like.

Descriptions: Upadhyay (1981, p. 72, Figs 217–222); Seifert & Okada (1993, p. 32, Fig. 3B).

Phylogenetic data: Gebhardt *et al.* (2004, 2005); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer *et al.* (2012).

Notes: This species is closely related to *O. bicolor* in the *O. ips* complex based on SSU sequences (Gebhardt *et al.* 2004, 2005; De Beer *et al*. 2012). Although the sequence does not come from the ex-type strain, the species is morphologically consistent with the *O. ips* complex based on its oblong, sheathed ascospores and anamorph, and should be considered in future treatments of that group.

Ophiostoma arduennense F.X. Carlier, Decock, K. Jacobs & Maraite, Mycol. Res. 110: 805. 2006.

Anamorph: unknown.

Phylogenetic data: Villarreal *et al.* (2005); Carlier *et al.* (2006); Kamgan Nkuekam *et al.* (2008a, 2010); Linnakoski *et al.* (2008, 2009); De Beer & Wingfield (2012).

Notes: This species groups close to *O. distortum*, peripheral to the *O. ulmi* complex (De Beer & Wingfield 2012).

Ophiostoma australiae (Kamgan, K. Jacobs & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. ***comb. nov.*, MB 801085** ≡ *Pesotum australiae* Kamgan, K. Jacobs & M.J. Wingf., Australasian Plant Path. 37: 410. 2008 [as *'australe'*] (basionym)

Anamorph: pesotum-like.

Description: Kamgan Nkuekam *et al.* (2008b, pp 410–412, Fig. 4).

Phylogenetic data: Kamgan Nkuekam *et al.* (2008b, 2010, 2011, 2012a); Linnakoski *et al.* (2009, 2010); Grobbelaar *et al.* (2009, 2011); Six *et al.* (2011); De Beer & Wingfield (2012).

Notes: Known only by its anamorph, this species is part of the *O. ulmi* complex (De Beer & Wingfield 2012).

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

Anamorph: sporothrix-like.

Phylogenetic data: Zhou *et al.* (2006); De Meyer *et al*. (2008); Roets *et al*. (2008, 2010); Lu *et al.* (2009a); De Beer & Wingfield (2012).

Notes: This species is a part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma bacillosporum (Butin & G. Zimm.) de Hoog & Scheffer, Mycologia 76: 297. 1984 [as *'bacillisporum'*] ≡ *Ceratocystis bacillospora* Butin & G. Zimm., Phytopathol. Z. 74: 281. 1972.

Anamorph: hyalorhinocladiella-like.

Description: Upadhyay (1981, p. 91, Figs 314–317).

Phylogenetic data: Hausner *et al.* (1993b); Villarreal *et al.* (2005); Carlier *et al.* (2006); Linnakoski *et al*. (2009); Kamgan Nkuekam *et al.* (2010); Paciura *et al.* (2010b); (De Beer & Wingfield 2012).

Notes: This species is part of the *O. ulmi* complex (De Beer & Wingfield 2012).

Ophiostoma bicolor R.W. Davidson & D.E. Wells, *In* Davidson, Mycologia 47: 63. 1955 ≡ *Ceratocystis bicolor* (R.W. Davidson & Wells) R.W. Davidson, Mycologia 50: 665. 1958.

Anamorph: hyalorhinocladiella-like.

Descriptions: Kotýnková-Sychrová (1966, pp 47, 52, Fig. 4); Griffin (1968, pp 696–699, Figs 76–79, Pl. I); Olchowecki & Reid (1974, p. 1695); Upadhyay (1981, p. 73, Figs 232–235); Yamaoka *et al.* (1997, p. 1220).

Phylogenetic data: Hausner *et al.* (1993b); Okada *et al.* (1998); Schroeder *et al.* (2001); Gebhardt *et al.* (2004, 2005); Massoumi-Alamouti *et al.* (2007, 2009); Lu *et al.* (2009a); Harrington *et al.* (2010); Linnakoski *et al*. (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).

Notes: Griffin (1968) mentioned three morphotypes of *O. bicolor*, but no DNA sequence data are available for these. This species is part of the *O. ips* complex (De Beer *et al*. 2012, De Beer & Wingfield 2012).

Ophiostoma borealis Kamgan, H. Solheim & Z.W. de Beer, *In* Kamgan Nkuekam *et al.*, Crypt. Mycol. 31: 295. 2010.

Synanamorphs: pesotum-like, sporothrix-like.

Phylogenetic data: Kamgan Nkuekam *et al.* (2010); Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Notes: Forms part of the *O. ulmi* complex (De Beer & Wingfield 2012).

Ophiostoma botuliforme Masuya, *In* Masuya *et al.*, Mycoscience 44: 304. 2003.

Anamorph: pesotum-like.

Notes: This species is morphologically similar to *O. allantosporum* (Masuya *et al.* 2003a), but without DNA sequence data it cannot be placed accurately in a clade within *Ophiostoma*.

Leptographium brachiatum (Kendrick) M.J. Wingf., Trans. Br. Mycol. Soc. 85: 92. 1985 ≡ *Verticicladiella brachiata* W.B. Kendr., Can. J. Bot. 40: 786. 1962.

Descriptions: Kendrick (1962, pp 786–789, Fig. 6, 9K); Jacobs & Wingfield (2001, pp 70–72, Figs 43–45).

Phylogenetic data: Jacobs *et al.* (2001d); Kim *et al.* (2004); Masuya *et al.* (2004); Massoumi Alamouti *et al.* (2006); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. De Beer & Wingfield (2012) showed that this species groups with *L. antibioticum* within *Ophiostoma s.l.* and not in *Leptographium* as previously suggested (Jacobs *et al.* 2001d).

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

Anamorph: sporothrix-like.

Phylogenetic data: Madrid *et al*. (2010); De Beer & Wingfield (2012).

Notes: This species is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Sporothrix brasiliensis Marimon, Gené, Cano & Guarro, *In* Marimon *et al.*, J. Clin. Microbiol. 45: 3203. 2007.

Phylogenetic data: Marimon *et al*. (2007, 2008); De Meyer *et al.* (2008); Madrid *et al*. (2010); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Sporothrix brasiliensis* groups in the *S. schenckii – O. stenoceras* complex as part of *Ophiostoma s.l.* (Marimon *et al*. 2007).

Ophiostoma breviusculum W.H. Chung, Yamaoka, Uzunovic, J.J. Kim, Mycologia 98: 805. 2006.

Anamorph: pesotum-like.

Phylogenetic data: Chung *et al.* (2006); Linnakoski *et al.* (2008, 2009); Bommer *et al*. (2009); Lu *et al.* (2009a); Kamgan Nkuekam *et al.* (2010); Linnakoski *et al.* (2010); Paciura *et al.* (2010b); De Beer & Wingfield (2012).

Notes: This species is closely related to *O. ssiori* in *Ophiostoma s.str.* (De Beer & Wingfield 2012).

Raffaelea brunnea (L.R. Batra) T.C. Harr., *In* Harrington *et al.*, Mycotaxon 111: 351. 2010 ≡ *Monilia brunnea* Verrall, J. Agr. Res. 66: 142. 1943 [*nom. illegit*., Art. 53. 1] ≡ *Ambrosiella brunnea* L.R. Batra, Mycologia 59: 980. 1967 .

Descriptions: Verrall (1943, pp 142–143, Fig. 5); Batra (1967, pp 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 (2012).

Notes: Teleomorph unknown. This species is part of the *R. lauricol*a complex in *Opiostoma s.l.* (De Beer & Wingfield 2012). The name should not be confused with *Monilia brunnea* J.C. Gilman & E.V. Abbott.

Ophiostoma brunneo-ciliatum Math.-Käärik, Medd. Skogsforskninginst. 43: 44. 1954 ≡ *Ceratocystis brunneo-ciliata* (Math.-Käärik) J. Hunt, Lloydia 19: 32. 1956.

Anamorph: pesotum-like (Okada *et al.* 1998).

Descriptions: Hunt (1956, p. 32); Upadhyay (1981, p. 74, Figs 236–241); Yamaoka *et al.* (1998, p. 371, Figs 11–15).

Phylogenetic data: Hausner & Reid (2003); Linnakoski *et al*. (2010); De Beer & Wingfield (2012).

Notes: This species is morphologically similar to *O. clavatum* but it groups with *O. ainoae* and *O. tapionis* close to *O. floccosum* in *Ophiostoma s.str*. (De Beer & Wingfield 2012).

Sporothrix brunneoviolaceae Madrid, Gené, Cano & Guarro, *In* Madrid *et al*., Mycologia 102: 1199. 2010.

Descriptions: Halmschlager & Kowalski (2003, Figs 1–11, as *S. inflata*); Madrid *et al.* (2010, pp 1198–1200, Fig. 2).

Phylogenetic data: Aghayeva *et al*. (2005 as *S. inflata* Clade IV); Madrid *et al*. (2010); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. See notes under *Sporothrix inflata*, below. The species groups with *O. fumeum* and *O. fasciatum* in a distinct lineage in *Ophiostoma s.l.* (De Beer & Wingfield 2012).

Ophiostoma brunneum (R.W. Davidson) Hausner & J. Reid, Can. J. Bot. 81: 874. 2003 ≡ *Ceratocystis brunnea* R.W. Davidson, Mycologia 50: 663. 1958.

Anamorph: hyalorhinocladiella-like.

Descriptions: Olchowecki & Reid (1974, p. 1709); Hausner & Reid (2003, pp 869–871).

Phylogenetic data: Hausner & Reid (2003); Villarreal *et al.* (2005); Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Notes: Considered closely related to *O. piliferum* by Griffin (1968) and Olchowecki & Reid (1974). Upadhyay (1981) treated it as a doubtful species, but Hausner & Reid (2003) reconfirmed that it is a good species, distinct from *O. piliferum*. It groups close to *O. canum* and *O. piceae* in *Ophiostoma s. str.* (De Beer & Wingfield 2012).

Ophiostoma californicum (DeVay, R.W. Davidson & Moller) Hausner, J. Reid & Klassen, Can. J. Bot. 71: 1264. 1993 ≡ *Ceratocystis californica* DeVay, R.W. Davidson & Moller, Mycologia 60: 639. 1968.

Anamorph: sporothrix-like.

Description: Upadhyay (1981, p. 92, Figs 318–324).

Phylogenetic data: Hausner *et al.* (1993b); Hausner & Reid (2003); Zanzot *et al*. (2010); De Beer & Wingfield (2012).

Notes: Treated as synonym of *O. longirostellatum* by de Hoog (1974), but shown to be a distinct species in the *O. pluriannulatum* complex based on LSU data (Hausner *et al.* 1993b, Hausner & Reid 2003, De Beer & Wingfield 2012). Thwaites *et al*. (2005) suggested that two isolates from California that were distinct from *O. pluriannulatum* based on ITS might represent *O. californicum*, but they did not include the ex-type isolate of this species in their study.

Ophiostoma candidum Kamgan, Jol. Roux & Z.W. de Beer, *In* Kamgan Nkuekam *et al*., Mycol. Progress 11: 526. 2012.

Anamorph: sporothrix-like.

Description: Kamgan Nkuekam *et al.* (2012a, pp 526–527, Fig. 5).

Phylogenetic data: Kamgan Nkuekam *et al.* (2012a); De Beer & Wingfield (2012).

Notes: This species is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma canum (Münch) Syd., *In* Sydow & Sydow, Annls mycol. 17: 43. 1919 ≡ *Ceratostomella cana* Münch, Naturw. Z. Forst. Landw. 5: 558. 1907 ≡ *Ceratocystis cana* (Münch) Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 ≡ *Pachnodium canum* H.P. Upadhyay & W.B. Kendr., Mycologia 67: 802. 1975 ≡ *Pesotum canum* (H.P. Upadhyay & W.B. Kendr.) G. Okada & Seifert, *In* Okada *et al.*, Can. J. Bot. 76: 1503. 1998.

Anamorph: pesotum-like.

Descriptions: Mathiesen (1950, pp 289–296, Figs 3–9); Mathiesen (1951, pp 210–212); Hunt (1956, p. 35); Kotýnková-Sychrová (1966, p. 51); Olchowecki & Reid (1974, p. 1709); Upadhyay (1981, p. 93); Seifert & Okada (1993, p. 32, Fig. 3F); Harrington *et al.* (2001, pp 119, 122).

Phylogenetic data: Hausner *et al.* (1993b); Harrington *et al.* (2001); Schroeder *et al.* (2001); Jacobs *et al.* (2003c); Jacobs & Kirisits (2003); Masuya *et al.* (2003b); Villarreal *et al.* (2005); Carlier *et al.* (2006); Chung *et al.* (2006); Zipfel *et al.* (2006); Linnakoski *et al.* (2008, 2010); Bommer *et al*. (2009); Lu *et al.* (2009a); Massoumi Alamouti *et al.* (2009); Grobbelaar *et al*. (2010); Kamgan Nkuekam *et al.* (2010); Paciura *et al.* (2010b); Zanzot *et al*. (2010); De Beer & Wingfield (2012).

Notes: The anamorph of *O. canum* is the type species of *Pachnodium* (Upadhyay & Kendrick 1975), currently treated as a synonym of *Ophiostoma*. *Ophiostoma canum* consists of more than one cryptic species in need of resolution, and groups close to *O. piceae*, *O. brunneum*, *O. breviusculum* and *O. flexuosum* (Linnakoski *et al.* 2010; De Beer & Wingfield 2012).

Ophiostoma carpenteri J. Reid & Hausner, *In* Hausner *et al.*, Can. J. Bot. 81: 42. 2003.

Anamorph: sporothrix-like.

Phylogenetic data: Hausner *et al.* (1993a) (as '*Ceratocystiopsis* sp. 1'); Zipfel *et al.* (2006); De Beer & Wingfield (2012).

Notes: Based on LSU data, *O. carpenteri* forms part of the *O. pluriannulatum* complex together with the morphologically similar *O. retusum* (De Beer & Wingfield 2012). These two species differ markedly from other species in the complex in terms of morphology and biology,y and their relationships should be explored further with sequences from more gene regions (Hausner *et al.* 2003; De Beer & Wingfield 2012).

Ophiostoma castaneae (Vanin & Solovjev) Nannf., *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934 ≡ *Ceratostomella castaneae* Vanin & Solovjev, *In* Solovjev, Bull. Plant Protection, Leningrad 5: 122. 1932 ≡ *Ceratocystis castaneae* (Vanin & Solovjev) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.

Anamorph: unknown.

Description: Potlajczuk & Schekunova (1985, p. 156).

Notes: Hunt (1956) considered this species inadequately known because he was unable to obtain material, but he noted that the protologue described a fungus that differed from any that he knew. The species is not mentioned by Upadhyay (1981). *Ophiostoma bacillosporum* is morphologically similar to this species (Butin & Zimmermann 1972; Upadhyay 1981). The name is valid and could be resurrected by neotypification (Art. 9.6) or epitypification (Art. 9.7). Considering its long perithecial necks (1.1–1.8 mm) (Solovjev 1932), the species could be a member of the *O. pluriannulatum* complex.

Ophiostoma catonianum (Goid.) Goid., Boll Staz. Patol. Veg. Roma 15: 125. 1935 ≡ *Ceratostomella catoniana* Goid., R.C. Accad. Lincei 21: 199. 1935 ≡ *Ceratocystis catoniana* (Goid.) C. Moreau, Rev. Myc. (Paris) Suppl. Co. 17: 22. 1952 = *Graphium pirinum* Goid., Boll. Staz. Patol. Veg. Roma 15: 132. 1935 ≡ *Pesotum pirinum* (Goid.) G. Okada & Seifert, *In* Okada *et al.*, Can. J. Bot. 76: 1504. 1998 = *Hyalodendron pirinum* Goid., Boll. Staz. Patol.

Veg. Roma 15: 136. 1935 ≡ *Sporothrix pirina* (Goid.) Morelet, Ann. Soc. Sci. Nat. Arch. Toulon et du Var 44: 110. 1992 [as *'pirinum'*]

Anamorph: pesotum- and sporothrix-like.

Description: Harrington *et al.* (2001, p. 126).

Phylogenetic data: Harrington *et al.* (2001); Jacobs *et al.* (2003c); Jacobs & Kirisits (2003); Masuya *et al.* (2003b); Villarreal *et al.* (2005); Carlier *et al.* (2006); Kamgan Nkuekam *et al.* (2008b, 2010); Linnakoski *et al.* (2008, 2009, 2010); Grobbelaar *et al.* (2009, 2011); Paciura *et al.* (2010b); De Beer & Wingfield (2012).

Notes: A *nomen dubium fide* Hunt (1956), but de Hoog (1974), Upadhyay (1981), Hutchison & Reid (1988a) and Przybyl & de Hoog (1989) all treated *O. cationum* as a synonym of *O. piceae.* Hunt (1956) was unable to identify the degenerated ex-type culture (CBS 263.35), but de Hoog (1974) identified the fungus from the sporothrix-like synanamorphs. Harrington *et al.* (2001) showed that *O. catonianum* is a distinct species, which is currently treated in the *O. ulmi* complex (De Beer & Wingfield 2012). Okada *et al.* (1998) considered *P. pirinum*, the anamorph described for *O. catonianum* by Goidànich (1935a), to be the anamorph of *O. quercus*. However, Harrington *et al.* (2001) distinguished between *O. catonianum* and *O. quercus* and thus Grobbelaar *et al.* (2009) re-introduced *P. pirinum* as the anamorph of *O. catonianum.*

Ophiostoma clavatum Math., Svensk. Bot. Tidskr. 45: 222. 1951 ≡ *Ceratocystis clavata* (Math.) Hunt, Lloydia 19: 37. 1956.

Anamorph: pesotum-like.

Descriptions: Mathiesen (1950, p. 298); Hunt (1956, pp 37–38); Upadhyay (1981, p. 136).

Notes: Upadhyay (1981) considered this a *nomen dubium* because there was no teleomorph on the type specimen. The protologue includes a good illustration and the name could thus be resurrected by epitypification (Art. 9.7). The species is morphologically similar to *O. brunneociliatum*, and is probably a distinct species of *Ophiostoma s.str.*

Ophiostoma columnare (Olchow. & J. Reid) Seifert & G. Okada, *In* Okada *et al.*, Can. J. Bot. 76: 1504. 1998 [as *'columnaris'*] ≡ *Ceratocystis columnaris* Olchow. & J. Reid, Can. J. Bot. 52: 1689. 1974 = *Ceratocystis ossiformis* Olchow. & J. Reid, Can. J. Bot. 52: 1692. 1974.

Anamorph: pesotum-like (Okada *et al.* 1998).

Descriptions: Olchowecki & Reid (1974, pp 1689–1690, Pl. VIII Figs 142–151); Upadhyay (1981, p. 76, Figs 247–252); Seifert & Okada (1993, p. 29, Fig. 1B).

Phylogenetic data: Hausner *et al.* (1993b); Mullineux *et al*. (2011) for *C. ossiformis*; (De Beer & Wingfield 2012).

Notes: The suggested synonymy of *C. ossiformis* with *O. columnare* (Upadhyay 1981) was accepted by Hausner *et al.* (1993b). The LSU sequence of *O. columnare* is identical to that of *O. bicolor* (Hausner *et al.* 1993b) and both specie are part of the *O. ips* complex (De Beer & Wingfield 2012).

Ophiostoma conicola Marm. & Butin, Sydowia 42: 195. 1990 [as *'conicolum'*]

Anamorph: sporothrix-like.

Description: Marmolejo & Butin (1993, pp 157–158, 166, Figs 5–9).

Phylogenetic data: Hausner *et al.* (1993b, 2000); Masuya *et al.* (2004); Villarreal *et al.* (2005); Zanzot *et al*. (2010); De Beer & Wingfield (2012).

Notes: This species is part of the *O. pluriannulatum* complex (De Beer & Wingfield 2012).

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

Anamorph: sporothrix-like (Hutchison & Reid 1988).

Description: Hutchison & Reid (1988a, p. 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 (2012).

Notes: Upadhyay (1981) considered this species a synonym of *O. tenellum*, but this was rejected by Hutchison & Reid (1988a) because of differences in the shape of ascospores. ITS sequence data for *O. coronatum* differ in 5 bp from *O. tenellum* and the two were treated as a distinct species by Villarreal *et al.* (2005). The two species group close to *O. nigricarpum* in a lineage now referred to as the *O. tenellum* complex (De Beer & Wingfield 2012).

Ophiostoma cupulatum (McNew & Harrington) Z.W. de Beer & M.J. Wingf. , ***comb. nov.,* MB 801086** ≡ *Pesotum cupulatum* McNew & Harrington, Mycologia 93: 121. 2001.

Synanamorphs: pesotum- and sporothrix-like.

Description: Paciura *et al.* (2010b, p. 84, Figs 6, 10, 14, 17).

Phylogenetic data: Harrington *et al*. (2001); Paciura *et al.* (2010b); De Beer & Wingfield (2012).

Notes: Harrington *et al*. (2001) described *P. cupulatum* as anamorph of *O. setosum* based on mating compatibility. ITS sequences of the ex-type strains of the two species differ by 12 bp (De Beer & Wingfield 2012). We thus consider the species phylogenetically distinct and transfer *P. cupulatum* to *Ophiostoma*. Sequences of isolates from China identified as *O. setosum* by Paciura *et al.* (2010b) match those of *P. cupulatum* and should be ascribed to this species.

Ophiostoma crenulatum (Olchow. & J. Reid) Hausner & J. Reid, Can. J. Bot. 81: 875. 2003 ≡ *Ceratocystis crenulata* Olchow. & J. Reid, Can. J. Bot. 52: 1681. 1974 ≡ *Ceratocystiopsis crenulata* (Olchow. & J. Reid) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 124. 1981.

Anamorph: hyalorhinocladiella-like (Upadhyay 1981).

Description: Upadhyay (1981, p. 124, Figs 445–448).

Phylogenetic data: Hausner & Reid (2003); Jacobs & Kirisits (2003); Hafez *et al*. (2012); De Beer & Wingfield (2012).

Notes: This species is closely related to *O. fasciatum* based on LSU sequences, in a distinct lineage in *Ophiostoma s. l.* (Hausner & Reid 2003, De Beer & Wingfield 2012). It also groups separately from other *Ophiostoma* spp. based on SSU (Hafez *et al*. 2012). *Ophiostoma crenulatum* and *O. fasciatum* share some morphological characters that are unique within the *Ophiostomatales* (De Beer & Wingfield 2012).

Ophiostoma denticiliatum Linnakoski, Z.W. de Beer & M.J. Wingf., Persoonia 23: 12. 2009.

Synanamorphs: pesotum- and sporothrix-like*.*

Phylogenetic data: Linnakoski *et al*. (2009, 2010); Kamgan Nkuekam *et al.* (2010); Grobbelaar *et al.* (2011); De Beer & Wingfield (2012).

Notes: This species is part of the *O. ulmi* complex (De Beer & Wingfield 2012).

Ophiostoma denticulatum (R.W. Davidson) Z.W. de Beer & M.J. Wingf. ***comb. nov.,* MB 801087** ≡ *Ceratocystis denticulata* R.W. Davidson, Mycologia 71: 1088. 1979.

Anamorph: sporothrix-like*.*

Notes: The new combination is based on the sporothrix-like anamorph and kidney-shaped ascospores*.* The species probably belong in the *S. schenckii – O.stenoceras* complex and clearly not to *Ceratocystis*. The name should not be confused with the parasitic nematode, *Ophiostoma denticulatum* Rudolphi, a name governed by the ICZN (Table 1).

Ophiostoma dentifundum Aghayeva & M. J. Wingf., Mycol. Res. 109: 1134. (2005).

Anamorph: sporothrix-like.

Phylogenetic data: Aghayeva *et al.* (2004, 2005); Roets *et al.* (2006, 2008, 2010); Zhou *et al.* (2006); De Meyer *et al*. (2008); Madrid *et al*. (2010); De Beer & Wingfield (2012).

Notes: This is a member of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Sporothrix dimorphospora (Roxon & S.C. Jong) Madrid, Gené, Cano & Guarro, *In* Madrid *et al*., Mycologia 102: 1199. 2010 ≡ *Humicola dimorphospora* Roxon & S.C. Jong, Can. J. Bot. 52: 517. 1974.

Descriptions: Roxon & Jong (1974, pp 517–519, Figs 1–9); Madrid *et al*. (2010, pp 1199–1201, Fig. 3).

Phylogenetic data: Aghayeva *et al*. (2005) as *S. inflata*; Madrid *et al*. (2010); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. See notes under *Sporothrix inflata*, below. The species is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma distortum (R.W. Davidson) de Hoog & Scheffer, Mycologia 76: 297. 1984 ≡ *Ceratocystis distorta* R.W. Davidson, Mycologia 63: 10. 1971.

Anamorph: sporothrix-like*.*

Descriptions: Butin & Zimmermann (1972, p. 285, Fig. 5E); Olchowecki & Reid (1974, p. 1709); Upadhyay (1981, p. 94, Figs 334–338).

Phylogenetic data: Hausner *et al.* (1993b); Hausner & Reid (2003); Villarreal *et al.* (2005); Zipfel *et al.* (2006); Linnakoski *et al*. (2009); De Beer & Wingfield (2012).

Notes: Upadhyay (1981) considered the anamorph of this species to be 'yeast-like', but the original description by Davidson (which mentions 'sterigmata') and Upadhyay's illustration suggest a sporothrix-like anamorph*.* This species groups with *O. arduennense,* peripheral to the *O. ulmi* complex in *Ophiostoma s. str.* (De Beer & Wingfield 2012).

Ophiostoma epigloeum (Guerrero) de Hoog, Stud. Mycol. 7: 45. 1974 ≡ *Ceratocystis epigloea* Guerrero, Mycologia 63: 921. 1971 [as *'epigloeum'*]

Anamorph: sporothrix-like (de Hoog 1974)*.*

Descriptions: de Hoog (1974, pp 45–47, Fig. 17); Upadhyay (1981, p. 95, Figs 339–343).

Phylogenetic data: Hausner *et al.* (1993b).

Notes: Based on an LSU sequence (not available in GenBank), *O. epigloeum* groups close to the *S. schenckii – O. stenoceras* complex (Hausner *et al.* 1993b).

Ophiostoma fasciatum (Olchow. & J. Reid) Hausner, J. Reid & Klassen, Mycol. Res. 97: 631. 1993 [as *'fasciata'*] ≡ *Ceratocystis fasciata* Olchow. & J. Reid, Can. J. Bot. 52: 1682. 1974 ≡ *Ceratocystiopsis fasciata* (Olchow. & J. Reid) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 120. 1981 = *Ceratocystis spinifera* Olchow. & J. Reid, Can. J. Bot. 52: 1686. 1974.

Anamorph: hyalorhinocladiella-like (Upadhyay 1981)*.*

Descriptions: Upadhyay (1981, p. 126, Figs 454–465); Marmolejo & Butin (1993, pp 162, 170, Figs 38–41).

Phylogenetic data: Hausner *et al.* (1993a); Hausner & Reid (2003); Plattner *et al.* (2009); De Beer & Wingfield (2012).

Notes: *Ophiostoma fasciatum* is closely related to the morphologically similar *O. crenulatum,* in a distinct lineage within *Ophiostoma s.l.* based on LSU sequences. No ITS data is available for *O. crenulatum*, but based on ITS *O. fasciatum* groups with *O. fumeum* and *S. brunneoviolaceae*, but with little statistical support and long branches separating the species (De Beer & Wingfield 2012).

Ophiostoma flexuosum H. Solheim, Nord. J. Bot. 6: 203. 1986.

Anamorph: hyalorhinocladiella-like.

Phylogenetic data: Hausner *et al.* (1993b); Villarreal *et al.* (2005); Zipfel *et al.* (2006); Linnakoski *et al*. (2009, 2010); Kamgan Nkuekam *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species is closely related to *O. canum* in *Ophiostoma s.str*. (De Beer & Wingfield 2012).

Ophiostoma floccosum Math., Svensk. Bot. Tidskr. 45: 219. 1951 ≡ *Ceratocystis floccosa* (Math.) J. Hunt, Lloydia 19: 36. 1956 = *Graphium aureum* Hedgc., Mo. Bot. Gard. Rep. 17: 94. 1906 ≡ *Pesotum aureum* (Hedgc.) McNew & T.C. Harr., *In* Harrington *et al.*, Mycologia 93: 119. 2001.

Anamorph: pesotum-like.

Descriptions: Mathiesen (1950, p. 297); Hunt (1956, pp 36–37); Harrington *et al.* (2001, pp 119, 121–122).

Phylogenetic data: Harrington *et al.* (2001); Schroeder *et al.* (2001); De Beer & Wingfield (2003d); Jacobs *et al.* (2003c); Jacobs & Kirisits (2003); Kim *et al.* (2003, 2005a); Masuya *et al.* (2003b); Thwaites *et al.* (2005); Villarreal *et al.* (2005); Carlier *et al.* (2006); Chung *et al.* (2006); Zhou *et al.* (2006); Zipfel *et al.* (2006); Romón *et al.* (2007); Kamgan Nkuekam *et al.* (2008a, b, 2010); Linnakoski *et al.* (2008, 2010); Bommer *et al*. (2009); Lu *et al.* (2009a, b); Massoumi Alamouti *et al.* (2009); Grobbelaar *et al*. (2010, 2011); Harrington *et al.* (2010); Linnakoski *et al.* (2010); Paciura *et al.* (2010b); Kim *et al.* (2011); (De Beer & Wingfield 2012).

Notes: *Ophiostoma floccosum* was treated as a synonym of *O. piceae* by de Hoog (1974), Hutchison & Reid (1988a), Przybyl & de Hoog (1989), and Seifert *et al.* (1993). Harrington *et al.* (2001) showed that *O. floccosum* is a distinct species based on morphology and ITS sequences. It groups in *Ophiostoma s. str.*, close to *O. ainoae*, *O. brunneo-ciliatum* and *O. tapionis* (De Beer & Wingfield 2012). Harrington *et al.* (2001) confirmed that *Graphium aureum* is the anamorph of *O. floccosum* and transferred it to *Pesotum*. The name *P. aureum* should not be confused with *L. aureum*, anamorph of *G. aurea.*

Ophiostoma fumeum Kamgan, Jol. Roux & Z.W. de Beer, *In* Kamgan Nkuekam *et al*., Mycol. Progress 11: 527. 2012.

Anamorph: sporothrix-like.

Description: Kamgan Nkuekam *et al.* (2012a, pp 527–528, Fig. 6).

Phylogenetic data: Kamgan Nkuekam *et al.* (2012a); De Beer & Wingfield (2012).

Notes: This species groups with *S. brunneoviolaceae* and *O. fasciatum* in a distinct lineage in *Ophiostoma s.l.* (De Beer & Wingfield 2012).

Ophiostoma fuscum Linnakoski, Z.W. de Beer & M.J. Wingf., Persoonia 25: 85. 2010.

Anamorph: hyalorhinocladiella- to pesotum-like.

Phylogenetic data: Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Notes: Although no teleomorph is known for this species, Linnakoski *et al*. (2010) described it in *Ophiostoma*. De Beer & Wingfield (2012) confirmed that it is part of the *O. ips* complex.

Ophiostoma fusiforme Aghayeva & M.J. Wingf., Mycologia 96: 875. 2004.

Anamorph: sporothrix-like.

Phylogenetic data: Aghayeva *et al.* (2004, 2005); Zhou *et al.* (2004b, 2006); Villarreal *et al.* (2005); Roets *et al.* (2006, 2008, 2010); Zipfel *et al.* (2006); De Meyer *et al*. (2008); Lu *et al.* (2009a); Linnakoski *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma gemellus Roets, Z.W. de Beer & Crous, Mycologia 100: 504. 2008.

Anamorph: sporothrix-like.

Phylogenetic data: Roets *et al*. (2008, 2010, 2012); De Beer & Wingfield (2012).

Notes: This species is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Sporothrix globosa Marimon, Gené, Cano & Guarro, *In* Marimon *et al.*, J. Clin. Microbiol. 45: 3203. 2007 = *Sporotrichum tropicale* D. Panja, N.C. Dey & L.M. Ghosh, Indian Med. Gaz. 82: 202. 1947 [*nom. inval*., Art. 36.1]

Phylogenetic data: Marimon *et al*. (2007, 2008); De Meyer *et al.* (2008); Madrid *et al*. (2010).

Notes: Teleomorph unknown. *Sporothrix tropicale* was listed as synonym of *S. schenckii* by de Hoog (1974), but the ex-type isolate groups with *S. globosa* (Marimon *et al.* 2007). *Sporothrix globosa* is part of the *S. schenckii – O. stenoceras* complex (Marimon *et al*. 2007; Madrid *et al*. 2010).

Ophiostoma gossypinum (R.W. Davidson) J. Taylor, Mycopath. Mycol. Appl. 38: 112. 1976 ≡ *Ceratocystis gossypina* R.W. Davidson, Mycologia 63: 12. 1971.

Anamorph: sporothrix-like.

Phylogenetic data: Hausner *et al.* (1993b); Hausner & Reid (2003); De Beer & Wingfield (2012).

Notes: Davidson (1971) distinguished *O. gossypinum* and *C. gossypina var. robusta* based on perithecium morphology but Upadhyay (1981) treated both as synonyms of *O. stenoceras*. Hausner & Reid (2003) showed that the LSU sequence of the ex-type isolate (ATCC 18999) of *O. gossypinum* is distinct from that of *O. stenoceras*, but the two species group closely together in the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

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

Anamorph: sporothrix-like.

Phylogenetic data: Hausner *et al.* (1993b); Mullineux *et al*. (2011); De Beer & Wingfield (2012).

Notes: This species groups with *O. ambrosium* in a distinct lineage in *Ophiostoma s.l.* (De Beer & Wingfield 2012).

Ophiostoma himal-ulmi Brasier & M.D. Mehrotra, Mycol. Res. 99: 211. 1995.

Synanamorphs: pesotum- and sporothrix-like.

Description: Harrington *et al.* (2001, p. 127).

Phylogenetic data: Brasier *et al.* (1998); Harrington *et al.* (2001); Jacobs *et al.* (2003c); Jacobs & Kirisits (2003); Masuya *et al.* (2003b); Gibb & Hausner (2005); Paoletti *et al.* (2005); Villarreal *et al.* (2005); Carlier *et al.* (2006); Kamgan Nkuekam *et al.* (2008a, b, 2010); Linnakoski *et al.* (2008, 2009, 2010); Grobbelaar *et al*. (2010, 2011); Paciura *et al.* (2010b); De Beer & Wingfield (2012).

Notes: This species is a part of the *O. ulmi* complex (De Beer & Wingfield 2012).

Sporothrix humicola de Mey., Z.W. de Beer & M.J. Wingf., Mycologia 100: 656. 2008.

Description: De Meyer *et al.* (2008, pp 656–657, Figs 4d–f).

Phylogenetic data: De Meyer *et al.* (2008); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species belongs to the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma hyalothecium (R.W. Davidson) Hausner, J. Reid & Klassen, Can. J. Bot. 71: 1264. 1993 ≡ *Ceratocystis hyalothecium* R.W. Davidson, Mem. N.Y. Bot. Gard. 28: 47. 1976.

Anamorph: Unknown.

Description: Upadhyay (1981, p. 78, Figs 257–261).

Phylogenetic data: Hausner *et al.* (1993b); Hausner & Reid (2003); De Beer & Wingfield (2012).

Notes: *Ophiostoma hyalothecium* groups belongs to the *O. ips* complex based on a short LSU sequence (De Beer & Wingfield 2012). Although no anamorph is known, the species has pillow-shaped ascospores similar to other species in the *O. ips* complex (Davidson 1976, Upadhyay 1981).

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

Description: de Hoog (1974, pp 34–36, Fig. 14).

Phylogenetic data: Aghayeva *et al*. (2005); De Meyer *et al.* (2008); Roets *et al*. (2008); Madrid *et al*. (2010); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. Aghayeva *et al*. (2005) showed that isolates initially identified as *S. lignivora* separated into four clades, one representing *S. inflata s.str.* The second group included the ex-type isolate of *Humicola dimorphospora*, which was subsequently transferred to *Sporothrix* by Madrid *et al.* (2010), while the same authors described the third group as *S. brunneoviolaceae*. The fourth group remains undescribed. *Sporothrix inflata s.str.* is a member of in the *S. schenckii – O. stenoceras* complex, and part of *Ophiostoma s.l.* (De Beer & Wingfield 2012).

Ophiostoma introcitrinum (Olchow. & J. Reid) Hausner, J. Reid & Klassen, Can. J. Bot. 71: 1264. 1993 ≡ *Ceratocystis introcitrina* Olchow. & J. Reid, Can. J. Bot. 52: 1706. 1974 ≡ *Hyalopesotum introcitrinum* H.P. Upadhyay & W.B. Kendr., Mycologia 67: 802. 1975 [as *'introcitrina'*] ≡ *Pesotum introcitrinum* (H.P. Upadhyay & W.B. Kendr.) G. Okada & Seifert, *In* Okada *et al.*, Can. J. Bot. 76: 1503. 1998.

Anamorph: pesotum-like.

Descriptions: Olchowecki & Reid (1974, p. 1706, Pl. XV Figs 283–293); Upadhyay (1981, p. 98, Figs 353–358); Kowalski & Butin (1989, pp 237–238); Seifert & Okada (1993, p. 32, Fig. 3C).

Phylogenetic data: Hausner *et al.* (1993b); De Beer & Wingfield (2012).

Notes: The anamorph of *O. introcitrinum* is the type of the anamorph genus *Hyalopesotum* (Upadhyay & Kendrick 1975) and groups closely with *O. minus* and *O. pseudominus* in *Ophiostoma s.str.* (De Beer & Wingfield 2012). Therefore, *Hyalopesotum* is treated as synonym of *Ophiostoma*.

Ophiostoma ips (Rumbold) Nannf., *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934 ≡ *Ceratostomella ips* Rumbold, J. Agric. Res. 43: 864. 1931 ≡ *Grosmannia ips* (Rumbold) Goid., Boll. Staz. Patol. Veg. Roma 16: 27. 1936 ≡ *Ceratocystis ips* (Rumbold) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 = *Scopularia rumboldii* Goid., Boll. Staz. Patol. Veg. Roma 16: 39. 1936 [*nom. invalid*., Art. 36.1]

Anamorph: pesotum- to hyalorhinocladiella-like.

Descriptions: Nisikado & Yamauti (1933, pp 507–515, Figs 3–4); Leach *et al.* (1934, pp 327–331, Figs 7, 9, 10); Rumbold (1936, pp 420–426, Figs 1–5); Goidànich (1937, pp 251–253); Siemaszko (1939, pp 20, 22–23, Pl. I Figs 1–5); Mathiesen-Käärik (1953, pp 45–47); Hunt (1956, pp 11, 30–32); Griffin (1968, pp 703–704); Olchowecki & Reid (1974, p. 1692, Pl. VI Fig. 120); Wingfield & Marasas (1980a, pp 66–68, Figs 4–10); Upadhyay (1981, p. 79); Hutchison & Reid (1988a, pp 66, 68–70); Zhao (1992, pp 85–86); Marmolejo & Butin (1993, pp 158, 167, Figs 10–13); Benade *et al.* (1995, pp 300–301, Figs 2–9).

Phylogenetic data: Hausner *et al.* (1993a, c, 2000); Hausner & Reid (2003); Kim *et al.* (2003, 2005a); Zhou *et al.* (2004b); Thwaites *et al.* (2005); Villarreal *et al.* (2005); Carlier *et al.* (2006); Zhou *et al.* (2006); Zipfel *et al.* (2006); Romón *et al.* (2007); Lu *et al.* (2009a); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Linnakoski *et al.* (2010); Matsuda *et al.* (2010); Paciura *et al.* (2010b); Zanzot *et al*. (2010); Kim *et al.* (2011); De Beer & Wingfield (2012).

Notes: The *O. ips* species complex is characterised by pillow-shaped ascospores and named after *O. ips* because it was the first species described in this complex. *Ophiostoma adjuncti* and *O. montium*, both considered synonyms of *O. ips* by Upadhyay (1981), were considered distinct by Harrington (1987) and Hausner *et al.* (1993b) respectively. Hausner *et al.* (2000) further distinguished between *O. ips* and *O. adjuncti*, Kim *et al.* (2003) between *O. ips* and *O. montium*, and Zhou *et al.* (2004b) between *O. ips* and *O. pulvinisporum*. Zhou *et al*. (2002, 2007) applied microsatellite markers to investigate the population diversity of *O. ips*.

Ophiostoma japonicum Yamaoka & M.J. Wingf., *In* Yamaoka *et al.*, Mycol. Res. 101: 1222. 1997.

Anamorph: pesotum-like (Harrington *et al.* 2001).

Phylogenetic data: Masuya *et al.* (2012); De Beer & Wingfield (2012).

Notes: *Ophiostoma japonicum* is morphologically similar to *O. arborea* (Yamaoka *et al.* 1997) and phylogenetically is part of the *O. ips* complex (Masuya *et al.* 2012, De Beer & Wingfield 2012).

Ophiostoma karelicum Linnakoski, Z.W. de Beer & M.J. Wingf., Mycol. Res. 112: 1483. 2008.

Synanamorphs: pesotum- and sporothrix-like.

Phylogenetic data: Linnakoski *et al.* (2008, 2009, 2010); Kamgan Nkuekam *et al.* (2010); Zanzot *et al*. (2010); Grobbelaar *et al.* (2011); De Beer & Wingfield (2012).

Notes: This species is part of the *O. ulmi* complex (De Beer & Wingfield 2012).

Ophiostoma kryptum K. Jacobs & Kirisits, Mycol. Res. 107: 1234. 2003.

Anamorph: hyalorhinocladiella- to pesotum-like.

Phylogenetic data: Jacobs & Kirisits (2003); Villarreal *et al.* (2005); Carlier *et al.* (2006); Kamgan Nkuekam *et al.* (2008a, b, 2010); Linnakoski *et al.* (2008, 2010); Bommer *et al*. (2009); Grobbelaar *et al*. (2010); De Beer & Wingfield (2012).

Notes: This species groups in *Ophiostoma s.str.* (De Beer & Wingfield 2012).

Raffaelea lauricola T.C. Harr., Fraedrich & Aghayeva, Mycotaxon 104: 401. 2008.

Descriptions: Fraedrich *et al.* (2008, pp. 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 (2012).

Notes: Teleomorph unknown. This species froms a clade with *R. brunnea* to form the *R. lauricol*a complex in *Opiostoma s.l.* (De Beer & Wingfield 2012).

Ophiostoma leucocarpum (R.W. Davidson) Z.W. de Beer & M.J. Wingf. ***comb. nov.,*** **MB 801088** ≡ *Ceratocystis leucocarpa* R.W. Davidson, Mycopath. Mycol. Appl. 28: 278. 1966.

Anamorph: sporothrix-like (Upadhyay 1981).

Descriptions: Upadhyay (1981, p. 99, Figs 359–362).

Notes: Upadhyay (1981) reported that Davidson informed him that the type material was lost. Fresh cultures of the species were isolated by Olchowecki & Reid (1974), which were used by Upadhyay (1981). Based on the sporothrix-like anamorph and reniform ascospores, this species was classified by Olchowecki & Reid (1974) in their ‘Pilifera group’ and by Upadhyay (1981) in section *Ophiostoma.* Both groups of species are now incorporated in *Ophiostoma s.l.* as defined here, but no DNA sequences are available to determine its exact placement. The species clearly belong in *Ophiostoma* rather than *Ceratocystis*.

Ophiostoma lignorum (Wollenw.) Goid., Boll Staz. Patol. Veg. Roma, n.s. 15: 157. 1935 ≡ *Ceratostomella lignorum* Wollenw., *In* Wollenweber & Stapp, Biol. Reichs. Land Forstw. Arb., Berlin 16: 310. 1928.

Synamorphs: pesotum- and sporothrix-like (inferred from protologue).

Notes: Hunt (1956) treated the species as of uncertain status, but suggested that it resembles *O. tetropii*. Upadhyay (1981) did not consider this species. This species from spruce is validly published, and clearly belongs in *Ophiostoma s.l.* A neotype would need to designated (Art. 9.6) to enable critical comparisons with other species of *Ophiostoma*.

Ophiostoma longicollum Masuya, *In* Masuya *et al.*, Mycoscience 39: 349. 1998.

Anamorph: sporothrix-like.

Notes: The ascospore and anamorph morphology of this species suggest a relationship with species such as *O. stenoceras* or *O. nigricarpum*, but sequence data are needed to confirm its correct placement in the *Ophiostomatales*.

Ophiostoma longiconidiatum Kamgan, K. Jacobs & Jol. Roux, *In* Kamgan Nkuekam *et al*., Fungal Diversity 29: 53. 2008.

Anamorph: sporothrix-like.

Phylogenetic data: Kamgan Nkuekam *et al.* (2008a); Linnakoski *et al*. (2009); Zanzot *et al*. (2010); De Beer & Wingfield (2012).

Notes: This species is part of the *O. pluriannulatum* complex (De Beer & Wingfield 2012).

Ophiostoma longirostellatum (Bakshi) Arx & E. Müll., Beitr. Kryptogamenflora Schweiz 2: 395. 1954 ≡ *Ceratocystis longirostellata* Bakshi, Mycol. Pap. 35: 11. 1951.

Anamorph: sporothrix-like.

Description: de Hoog (1974, pp 61–62, Fig. 23).

Phylogenetic data: Hausner *et al.* (1993b, 2000); Masuya *et al.* (2004); Mullineux *et al*. (2011); De Beer & Wingfield (2012).

Note: This species was treated by Hunt (1956) as a synonym of *O. capillifera*, and by Upadhyay (1981, as '*O. longirostratum*') and Hutchison & Reid (1988a) as a synonym of *O. piliferum*. Hausner *et al.* (1993b) showed it is distinct from *O. piliferum*. It is part of the *O. pluriannulatum* complex (De Beer & Wingfield 2012).

Ophiostoma lunatum D.N. Aghayeva & M.J. Wingf., Mycologia 96: 874. 2004.

Anamorph: sporothrix-like.

Phylogenetic data: Aghayeva *et al.* (2004, 2005); Zhou *et al.* (2004b, 2006); Villarreal *et al.* (2005); Roets *et al.* (2006, 2008, 2010); Zipfel *et al.* (2006); De Meyer *et al*. (2008); Lu *et al.* (2009a); Linnakoski *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species groups with *O. fusiforme* in the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Sporothrix luriei (Ajello & Kaplan) Marimon, Gené, Cano & Guarro, Med. Mycol. 46: 624. 2008 ≡ *S. schenckii var. luriei* Ajello & Kaplan, Mykosen 12: 642. 1969.

Descriptions: Ajello & Kaplan (1969, pp 642–643, Figs 2–20); Marimon *et al.* (2008, pp 623–624, Fig. 2).

Phylogenetic data: Marimon *et al.* (2008); Madrid *et al*. (2010); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma macrosporum (Francke-Grosm.) Z.W. de Beer & M.J. Wingf. ***comb. nov.,* MB 801089** ≡ *Trichosporum tingens var. macrosporum* Francke-Grosm., Medd. Skogsforskninginst. 41: 27. 1952 [as *'Trichosporium tingens var. macrosporum'*] (basionym) ≡ *Ambrosiella macrospora* (Francke-Grosm.) L.R. Batra, Mycologia 59: 980. 1967 ≡ *Hyalorhinocladiella macrospora* (Francke-Grosm.) TC. Harr., *In* Harrington *et al.*, Mycotaxon 111: 355. 2010.

Anamorph: hyalorhinoclaidella- to raffaelea-like.

Description: Batra (1967, pp 1007–1008, Figs 47, 48).

Phylogenetic data: Cassar & Blackwell (1996); Rollins *et al.* (2001); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).

Notes: Forms a distinct lineage together with *O. tingens* in *Ophiostoma s.str.* (De Beer & Wingfield 2012). The arguments for the new combination are outlined under Lineage B in De Beer & Wingfield (2012).

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

Synanamorphs: sporothrix- and yeast-like (Upadhyay 1981).

Description: Upadhyay (1981, p. 100, Figs 363–365).

Notes: The synanamorphs of this species were not illustrated in the protologue, nor by Upadhyay (1981). Morphology of the ascospores and the descriptions of the sporothrix-like anamorph suggest that it might be part of the *S. schenckii – O. stenoceras* complex, but it should be re-examined and sequenced.

Sporothrix mexicana Marimon, Gené, Cano & Guarro, *In* Marimon *et al.*, J. Clin. Microbiol. 45: 3203. 2007*.*

Description: Marimon *et al.* (2007, pp 3203–3204, Fig. 2E).

Phylogenetic data: Marimon *et al.* (2007, 2008); De Meyer *et al.* (2008); Madrid *et al*. (2010).

Notes: Teleomorph unknown. This species was not considered by De Beer & Wingfield (2012), but according to Madrid *et al*. (2010) it belongs to the *S. schenckii – O. stenoceras* complex.

Ophiostoma microsporum Arx, Antonie van Leeuwenhoek 18: 211. 1952 ≡ *Ceratostomella microspora* R.W. Davidson, Mycologia 34: 650. 1942 [*nom. illegit.*, Art. 52.1, later homonym for *Cs. microspora* Ellis & Everh., see Section C.1] ≡ *Ceratocystis perparvispora* J. Hunt, Lloydia 19: 46. 1956 [superfluous *nom. nov.*] ≡ *Ceratocystis microspora* (R.W. Davidson) R.W. Davidson & Aoshima, Ph.D. thesis, University of Tokyo: 20. 1965 [*nom. inval*., Art. 29.1, 36.1] ≡ *Ceratocystis microspora* (Arx) R.W. Davidson, J. Col.-Wyom. Acad. Sci. 6: 16. 1969.

Anamorph: sporothrix-like*.*

Descriptions: Hunt (1956, pp 46–47); Griffin (1968, p. 710); de Hoog (1974, pp 63–64, Fig. 25); Olchowecki & Reid (1974, p. 1709); Upadhyay (1981, p. 50, Figs 104–108); Maekawa *et al.* (1987, pp 8, 10, Figs 1–6).

Phylogenetic data: Hausner *et al*. (1993b); Mullineux *et al*. (2011); De Beer & Wingfield (2012).

Note: The confusing taxonomy of this species (Davidson & Kuhlman 1978) was clarified by Weresub (1979). The LSU sequence for isolate CBS 412.77 generated by Hausner *et al*. (1993b), is identical to the sequence produced by De Beer & Wingfield (2012) of the ex-neotype isolate (CBS 440.69 = CMW 17152) designated by Davidson & Kuhlman (1978). The species groups between *Raffaelea s.str*. and *Ophiostoma s.str.* in its own lineage. Its generic placement remains uncertain (De Beer & Wingfield 2012). The name *O. microsporum* should not be confused with *L. microsporum* (see under *Leptographium*), nor *Cs. microspora* (see section C.2).

Ophiostoma minus (Hedgc.) Syd., *In* Sydow & Sydow, Annls mycol. 17: 43. 1919 [as '*minor*'] ≡ *Ceratostomella minor* Hedgc., Mo. Bot. Gard. Ann. Rep. 17: 74. 1906 ≡ *Ceratocystis minor* (Hedgc.) J. Hunt, Lloydia 19: 47. 1956 = *Ceratostomella exigua* Hedgc., Mo. Bot. Gard. Ann. Rep. 17: 76. 1906 ≡ *Ophiostoma exiguum* (Hedgc.) Syd., Annls mycol. 17: 43. 1919 = *Ceratostomella pini* Münch, Naturwiss. Z. Forst. Landw. 5: 541. 1907 ≡ *Ophiostoma pini* (Münch) Syd., Annls mycol. 17: 43. 1919 ≡ *Grosmannia pini* (Münch) Goid., Boll. Staz. Patol. Veg. Roma 16: 27. 1936 ≡ *Scopularia pini* Goid., Boll. Staz. Patol. Veg. Roma 16: 39. 1936 [*nom. invalid*., Art. 36.1] ≡ *Ceratocystis pini* (Münch) C. Moreau, Rev. Mycol. (Paris), Suppl. Colon. 17: 22. 1952.

Anamorph: hyalorhinocladiella-like.

Descriptions: Lagerberg *et al*. (1927, pp 189–196, Figs 17–21 as *C. pini*); Rumbold (1931, pp 851–862 as *C. pini*); Nisikado & Yamauti (1934 pp 470–474, Plates 17–21, as *Cs. pini*); Siemaszko (1939, pp 20, 31–32 as *O. pini*); Hunt (1956, pp 11, 47–48); Kotýnková-

Sychrová (1966, p. 52); Griffin (1968, p. 704); Olchowecki & Reid (1974, p. 1707, Pl. XVI Fig. 314); Upadhyay (1981, p. 100); Potlajczuk & Schekunova (1985, p. 153); Benade *et al.* (1996, pp 894–895, Figs 11–14).

Phylogenetic data: Gorton & Webber (2000); Jacobs & Kirisits (2003); Gorton *et al.* (2004); Villarreal *et al.* (2005); Carlier *et al.* (2006); Romón *et al.* (2007); Lu *et al.* (2009a); Kamgan Nkuekam *et al.* (2010); Linnakoski *et al*. (2010); Paciura *et al.* (2010b); De Beer & Wingfield (2012); Hafez *et al.* (2012).

Note: Hunt (1956), Griffin (1968), Olchowecki & Reid (1973) and Upadhyay (1981) treated *O. exiguum*, *O. pini*, and *O. pseudotsugae* as synonyms of *O. minus*. However, Gorton & Webber (2000) and Gorton *et al.* (2004) showed *O. pseudotsugae* to be distinct.

Rumbold (1931) reported *O. pini* from the USA. She distinguished between strains from the east and west coasts, and a third type from Washington, D.C., which she suggested was the same as the European *O. pini*. She considered *O. exiguum* and *O. minus* to be distinct, based on studies of her own isolates. Mathiesen (1950) also differentiated her own *O. pini* isolates from Sweden from those described from the USA by Rumbold (1931). Gorton & Webber (2000), Gorton *et al.* (2004), Lu *et al.* (2009a) and Linnakoski *et al*. (2010) confirmed that *O. minus* consists of at least two phylogenetic species grouping according to geographical origin, a North American species (*O. minus*) and the European species. The two species group closely together in *Ophiostoma s. str*. (De Beer & Wingfield 2012). Epitypification of *O. pini* and *O. exiguum* would be necessary to resolve their status and the appropriate name for the European isolates. Thus, we have treated *O. pini* and *O. exiguum* as synonyms of *O. minus* until that research has been completed.

The name *O. pini s*hould not be confused with *P. pini*, a synonym of *G. radiaticola*.

Ophiostoma montium (Rumbold) Arx, Antonie van Leeuwenhoek 18: 211. 1952 ≡ *Ceratostomella montium* Rumbold, J. Agric. Res. 62: 597. 1941 ≡ *Ceratocystis montia* (Rumbold) J. Hunt, Lloydia 19: 45. 1956 = *Tuberculariella ips* J.G. Leach, L.W. Orr & C.M. Chr., J. Agr. Res. 49: 335. 1934 ≡ *Ambrosiella ips* (J.G. Leach, L.W. Orr & C.M. Chr.) L.R. Batra, Mycologia 59: 980. 1967 ≡ *Hyalorhinocladiella ips* (J.G. Leach, L.W. Orr & C.M. Chr.) T.C. Harr., Mycotaxon 111: 355. 2010.

Anamorph: pesotum- to hyalorhinocladiella-like.

Descriptions: Leach *et al.* (1934, pp 331–336, Figs 11–12 of *Tu. ips*); Taylor-Vinje (1940, pp 764–773, Figs 1–30); Rumbold (1941, pp 591–597, Figs 2–5); Hunt (1956, pp 45–46).

Phylogenetic data: Hausner *et al.* (1993b); Cassar & Blackwell (1996); Rollins *et al.* (2001); Kim *et al.* (2003); Zhou *et al.* (2004b); Gebhardt *et al.* (2005); Zipfel *et al.* (2006); Lu *et al.* (2009a); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Linnakoski *et al.* (2010); Matsuda *et al.* (2010); Paciura *et al.* (2010b); Zanzot *et al*. (2010); Roe *et al.* (2011); De Beer & Wingfield (2012).

Note: *Ophiostoma montium* was treated as a synonym of *O. ips* by Upadhyay (1981) and Hutchison & Reid (1988a), but Hausner *et al*. (1993b), Kim *et al.* (2003) and Zhou *et al.* (2004b) distinguished between *O. ips* and *O. montium*.

Massoumi Alamouti *et al*. (2009) suggested that *A. ips* might be the anamorph of *O. montium* based on DNA ssequences and morphological similarities. Harrington *et al*. (2010) then transferred *A. ips* to *Hyalorhinocladiella*. However, SSU, LSU, and β-tubulin sequences of the ex-type isolate of *A. ips* (CBS 435.34) differ by 0, 2 and 1 bp respectively when compared to available sequences of more than 80 isolates of *O. montium* from the studies of Kim *et al.* (2003), Gebhardt *et al*. (2005), Massoumi Alamouti *et al*. (2009), and Roe *et al*. (2011). We therefore support the synonymy suggested by Massoumi Alamouti *et al*. (2009). Although the epithet of *Tu. ips* is older that for *Cs. montium,* the epithet *ips* is already occupied in *Ophiostoma* and transferring *T. ips* to *Ophiostoma* would create a later homonym (*nom. illegit*., Art. 53.1)*,* and therefore the continued use of *O. montium* is necessary.

Ophiostoma montium was included in a four gene phylogeographic study, showing that it reproduces sexually in nature (Roe *et al.* 2011).

Ophiostoma multiannulatum (Hedgc. & R.W. Davidson) Hendrix, Ann. Gembloux 33: 99. 1937 ≡ *Ceratostomella multiannulata* Hedgc. & R.W. Davidson, *In* Davidson, J. Agric. Res. 50: 797. 1935 ≡ *Ophiostoma multiannulatum* (Hedgc. & R.W. Davidson) N. Fries, Symb. Bot. Upsal. 7: 21. 1943 [*nom. illegit.*, Art. 52.1] ≡ *Ophiostoma multiannulatum* (Hedgc. & R.W. Davidson) Arx, Antonie van Leeuwenhoek 18: 211. 1952 [*nom. illegit.*, Art. 52.1] ≡ *Ceratocystis multiannulata* (Hedgc. & R.W. Davidson) J. Hunt, Lloydia 19: 40. 1956.

Anamorph: sporothrix-like.

Descriptions: Hunt (1956, pp 11, 17, 40–41); de Hoog (1974, p. 53); Upadhyay (1981, p. 102, Figs 371–377).

Phylogenetic data: Villarreal *et al.* (2005); Zhou *et al.* (2006); Zipfel *et al.* (2006); Kamgan Nkuekam *et al.* (2008a, b); Linnakoski *et al*. (2009); Paciura *et al.* (2010b); Zanzot *et al*. (2010); De Beer & Wingfield (2012).

Notes: This species is part of the *O. pluriannulatum* complex (De Beer & Wingfield 2012).

Ophiostoma narcissi Limber, Phytopathology 40: 493. 1950 ≡ *Ceratocystis narcissi* (Limber) J. Hunt, Lloydia 19: 50. 1956.

Anamorph: sporothrix-like.

Descriptions: Hunt (1956, pp 11, 50); de Hoog (1974, pp 59–60, Fig. 22); Olchowecki & Reid (1974, p. 1707, Pl. XVI Fig. 316); Upadhyay (1981, p. 103).

Phylogenetic data: De Beer *et al.* (2003b); Hausner & Reid (2003); Jacobs *et al.* (2003c); Villarreal *et al.* (2005); Zhou *et al.* (2006); Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Notes: *Ophiostoma narcissi* is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

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

Anamorph: sporothrix-like.

Descriptions: de Hoog (1974, pp. 62–63, Fig. 24); Olchowecki & Reid (1974, p. 1709); Upadhyay (1981, p. 104 Figs 378–381); Benade *et al.* (1997, pp. 1110–1111, Figs 6–11).

Phylogenetic data: Aghayeva *et al.* (2004); Zhou *et al.* (2004b, 2006); Roets *et al.* (2006, 2008, 2010); Zipfel *et al.* (2006); De Meyer *et al*. (2008); Linnakoski *et al.* (2010); Madrid *et al*. (2010).

Notes: De Beer *et al.* (2003b) incorrectly identified several isolates of *O. abietinum* as *O. nigricarpum*. Aghayeva *et al.* (2004) showed that the ex-type strain of *O. nigricarpum* is distinct from *O. abietinum.* It is part of the *O. tenellum* complex (De Beer & Wingfield 2012).

Ophiostoma nigrogranum Masuya, Mycoscience 45: 278. 2004.

Anamorph: sporothrix-like.

Notes: Listed by Masuya *et al.* (2012) as part of *S. schenckii – O. stenoceras* complex, but this should be confirmed based on phylogenetic inference.

Ophiostoma nikkoense Yamaoka & Masuya, *In* Yamaoka *et al.*, Mycoscience 45: 278. 2004.

Anamorph: pesotum-like.

Phylogenetic data: De Beer & Wingfield (2012); Masuya *et al.* (2012).

Notes: ITS sequence data place this species with septate conidia in *Ophiostoma s. str.* (Masuya *et al.* 2012, De Beer & Wingfield 2012).

Ophiostoma nothofagi (Butin) Rulamort, Bull. Soc. Bot. Centre-Ouest, n.s. 17: 192. 1986 ≡ *Ceratocystis nothofagi* Butin, *In* Butin & Aquilar, Phytopathol. Z. 109: 84. 1984.

Anamorph: sporothrix-like.

Notes: The cultural morphology of this species suggests that it is related to species such as *O. piliferum* or *O. pluriannulatum* rather than to the *S. schenckii – O. stenoceras* complex.

Ophiostoma novo-ulmi Brasier, Mycopathologia 115: 155. 1991.

Anamorph: pesotum- and sporothrix-like*.*

Description: Harrington *et al.* (2001, p. 127).

Phylogenetic data: Bates *et al.* (a, b); Jeng *et al.* (1996); Brasier *et al.* (1998); Harrington *et al.* (2001); Jacobs *et al.* (2003c); Jacobs & Kirisits (2003); Masuya *et al.* (2003); Hausner *et al.* (2005a); Gibb & Hausner (2005); Paoletti *et al.* (2005); Villarreal *et al.* (2005); Carlier *et al.* (2006); Chung *et al.* (2006); Zipfel *et al.* (2006); Kamgan Nkuekam *et al.* (2008a, b, 2010); Linnakoski *et al.* (2008, 2009, 2010); Bommer *et al*. (2009); Massoumi Alamouti *et al.* (2009); Grobbelaar *et al*. (2010, 2011); Paciura *et al.* (2010b); De Beer & Wingfield (2012).

Notes: *Ophiostoma novo-ulmi* is part of the *O. ulmi* complex (De Beer & Wingfield 2012). According to strict application of Art. 60.9, the epithet for this species should be *novoülmi* (W. Gams, *in. litt.*). Despite this, we propose to maintain the hyphenated version of the epithet of this very important fungus because of its predominance in the literature, where the formally corrected version has never been used. This hyphenated spelling will be included in the eventual *List of Protected Names* for the *Ophiostomatales*, and we hope it will be approved by the Nomeclature Committee for Fungi.

Several studies have shown that two biological groups, termed EAN and NAN races, exist within *O. novo-ulmi* (Brasier 1979; Bates *et al.* 1993a, b; Solla *et al.* 2008). Brasier & Kirk (2001) designated these two groups as subspecies:

Ophiostoma novo-ulmi Brasier subsp. *novo-ulmi*, *In* Brasier & Kirk, Mycol. Res. 105: 549. 2001

Ophiostoma novo-ulmi subsp. *americana*, Brasier & S.A. Kirk, Mycol. Res. 105: 550. 2001

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

Descriptions: Kreisel & Shauer (1985, pp 654–657, Figs 1–4); Matsushima (1975, p. 143, Plate 163).

Phylogenetic data: Marimon *et al*. (2007, 2008); Madrid *et al*. (2010); De Meyer *et al.* (2008); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Calcarisporium pallidum* and *S. albicans* were listed as synonyms of *S. schenckii* by de Hoog (1974). However, De Meyer *et al*. (2008) showed that these two species and *S. nivea* group together in a lineage distinct from *S. schenckii,* based on β-tubulin sequences. They thus synonymised *S. albicans* and *S. nivea* with *S. pallida*. No teleomorph is known for this species, which belongs to the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma pallidulum Linnakoski, Z.W. de Beer & M.J. Wingf., Persoonia 25: 86. 2010.

Anamorph: hyalorhinocladiella-like.

Phylogenetic data: Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Notes: Teleomorph not observed. The species groups with *O. saponiodorum* in a distinct lineage within *Ophiostoma s.l.* (Linnakoski *et al*. 2010; De Beer & Wingfield 2012).

Ophiostoma palmiculminatum Roets, Z.W. de Beer & M.J. Wingf., Stud. Mycol. 55: 208. 2006.

Anamorph: sporothrix-like.

Phylogenetic data: Roets *et al.* (2006, 2008, 2010, 2012); De Meyer *et al*. (2008); Madrid *et al*. (2010); De Beer & Wingfield (2012).

Notes: This species is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma perfectum (R.W. Davidson) de Hoog, Stud. Mycol. 7: 54. 1974 ≡ *Ceratocystis perfecta* R.W. Davidson, Mycologia 50: 665. 1958.

Synanamorphs: pesotum- and sporothrix-like (de Hoog 1974).

Descriptions: de Hoog (1974, pp 54–55, Fig. 20); Olchowecki & Reid (1974, p. 1707, Pl. XVI Figs 305–306, 309–310); Upadhyay (1981, p. 105).

Phylogenetic data: Thwaites *et al.* (2005); Villarreal *et al.* (2005); Kamgan Nkuekam *et al.* (2008b); Zanzot *et al*. (2010).

Notes: This species was considered distinct by de Hoog (1974), Olchowecki & Reid (1974) and Upadhyay (1981). Przybyl & de Hoog (1989) and Seifert *et al.* (1993) treated it a synonym of *O. piceae.* Davidson (1958) did not mention a synnematous anamorph in the original description, while de Hoog (1974) described both synnemata and a sporothrix-like anamorph from the ex-type isolate (CBS 636.66). ITS sequences of the same generated strain by different authors do not correspond. Thwaites *et al.* (2005) showed that it (DQ062970) groups close to *O. pluriannulatum*, while the sequence of Villarreal *et al.* (2005) (AY934514) is close *O. floccosum.* These observations suggest that the ex-type culture might have been mixed; it should be re-examined to clarify the placement of the species in *Ophiostoma s.l.*

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

Anamorph: sporothrix-like*.*

Notes: The morphological description suggests that this is a good species of *Ophiostoma,* and probably part of the *S. schenckii – O. stenoceras* complex. As far as we could establish, no type material exists and neotypification is not recommended at this time.

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

Anamorph: sporothrix-like.

Phylogenetic data: Roets *et al.* (2006, 2008, 2010, 2012); De Meyer *et al*. (2008); Madrid *et al*. (2010); De Beer & Wingfield (2012).

Notes: This is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma piceae (Münch) Syd., *In* Sydow & Sydow, Annls mycol. 17: 43. 1919 ≡ *Ceratostomella piceae* Münch, Naturw. Land. Forstw. 5: 547. 1907 ≡ *Ceratocystis piceae* (Münch) Bakshi, Trans. Br. Mycol. Soc. 33: 113. 1950 ≡ *Pesotum piceae* Crane & Schoknecht, Am. J. Bot. 60: 348. 1973 ≡ *Graphium piceae* (Crane & Schoknecht) M.J. Wingf. & W.B. Kendr., Mycol. Res. 95: 1331. 1991.

Synannamorphs: pesotum- and sporothrix-like.

Descriptions: Only descriptions from studies that distinguish *O. piceae* and *O. quercus* are listed: Mouton *et al.* (1993, pp 374–375, Figs 9–12, 14); Seifert & Okada (1993, p. 33, Figs 4C-D); Halmschlager *et al.* (1994, pp 556–557); Benade *et al.* (1997, p. 1110, Figs 3–5); Harrington *et al.* (2001, pp 117–119), Jacobs *et al.* (2003c, p. 322, Figs 2–6); Paciura *et al.* (2010b, pp 82, 84, Figs 5, 9, 13, 16).

Phylogenetic data: Hausner *et al.* (1993c, 2000, 2005a); Halmschlager *et al.* (1994); Kim *et al.* (1999, 2003, 2005a); Okada *et al.* (1998); Harrington *et al.* (2001); Kim & Breuil (2001); Schroeder *et al.* (2001); De Beer *et al.* (2003d); Hausner & Reid (2003); Jacobs *et al.* (2003c); Jacobs & Kirisits (2003); Masuya *et al.* (2003b, 2004); Gebhardt *et al.* (2005)*;* Thwaites *et al.* (2005); Villarreal *et al.* (2005); Carlier *et al.* (2006); Chung *et al.* (2006); Zipfel *et al.* (2006); Romón *et al.* (2007); Kamgan Nkuekam *et al.* (2008a, b, 2010); Linnakoski *et al.* (2008, 2009, 2010); Bommer *et al*. (2009); Lu *et al.* (2009a, b); Massoumi Alamouti *et al.* (2009); Grobbelaar *et al*. (2010, 2011); Harrington *et al.* (2010); Matsuda *et al.* (2010); Paciura *et al.* (2010b); Zanzot *et al*. (2010); Kim *et al.* (2011); De Beer & Wingfield (2012).

Notes: A broad concept was applied to this species for many years, until mating studies, biological differences and DNA sequence data delineated *O. piceae* as a conifer-inhabiting species, distinct from hardwood species like *O. quercus* (Morelet 1992; Brasier & Kirk 1993;

Brasier & Stephens 1993; Harrington *et al*. 2001). De Beer & Wingfield (2012) showed that the conifer clade of the '*O. piceae* complex' is not monophyletic, but the species previously considered part of this complex all group in *Ophiostoma s.str.*

Ophiostoma piliferum (Fr. : Fr.) Syd., *In* Sydow & Sydow, Annls mycol. 17: 43. 1919 ≡ *Sphaeria pilifera* Fr., Syst. Mycol. 2(2): 472. 1822 ≡ *Ceratostoma piliferum* (Fr.) Fuckel, Symb. Mycol. p. 128. 1869 ≡ *Ceratostomella pilifera* (Fr.) G. Winter, Rabenh. Kryptogamen-Flora 1: 252. 1887 ≡ *Linostoma piliferum* (Fr.) Höhn., Annls mycol. 16: 91. 1918 ≡ *Ceratocystis pilifera* (Fr.) C. Moreau, Rev. Mycol. (Paris), Suppl. Colon. 17: 22. 1952 = *Ceratostomella capillifera* Hedgc., Mo. Bot. Gard. Ann. Rep. 17: 71. 1906 ≡ *Ophiostoma capilliferum* (Hedgc.) Syd., *In* Sydow & Sydow, Annls mycol. 17: 43. 1919 ≡ *Ceratocystis capillifera* (Hedgc.) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 = *Ceratostomella schrenkiana* Hedgc., Mo. Bot. Gard. Ann. Rep. 17: 67. 1906 ≡ *Ophiostoma schrenkianum* (Hedgc.) Syd., *In* Sydow & Sydow, Annls mycol. 17: 43. 1919 ≡ *Ceratocystis schrenkiana* (Hedgc.) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 = *Ceratostomella coerulea* Münch, Naturw. Land. Forstw. 5: 561. 1907 ≡ *Ophiostoma coeruleum* (Münch) Syd., *In* Sydow & Sydow, Annls mycol. 17: 43. 1919 ≡ *Ceratocystis coerulea* (Münch) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.

Anamorph: sporothrix-like (de Hoog 1974).

Descriptions: Von Schrenk (1903, pp 22–23, Pl. 7 Figs 4–9); Hedgcock (1906, pp 64–67, Pl. 3 Fig. 8, Pl. 4 Figs 5–7); Lagerberg *et al*. (1927, pp 163–174, Figs 1–8 as *C. coerulea*); Goidànich (1937, pp 226–242, Figs 1–13); Siemaszko (1939, pp 20, 29–30, Pl. I Figs 6–7); Hunt (1956, pp 11, 15, 41–42); Kotýnková-Sychrová (1966, p. 52); Griffin (1968, pp 711–712); de Hoog (1974, pp 47–50, Fig. 18); Olchowecki & Reid (1974, p. 1707, Pl. XVI Fig. 313); Upadhyay (1981, p. 107, Figs 382–386); Butin & Aquilar (1984, pp 83–84); Hutchison & Reid (1988a, pp 75–77); Marmolejo & Butin (1993, pp 160–161, 168, Figs 23–27); Benade *et al.* (1998, pp 256–257, Figs 2–4).

Phylogenetic data: Hausner *et al.* (1993c, 2000); Schroeder *et al.* (2001, 2002); Hausner & Reid (2003); Jacobs & Kirisits (2003); Kim *et al.* (2003, 2005a); Gorton *et al.* (2004); Masuya *et al.* (2004); Gebhardt *et al.* (2005); Zipfel *et al.* (2006); Zhou *et al.* (2006); Tang *et al.* (2007); Kamgan Nkuekam *et al.* (2008a, b, 2010); Linnakoski *et al.* (2008, 2009, 2010); Lu *et al.* (2009b); Grobbelaar *et al*. (2010); Harrington *et al.* (2010); Paciura *et al.* (2010b); Zanzot *et al*. (2010); De Beer *et al*. (2012).

Note: Schroeder *et al.* (2001, 2002) and Hausner & Reid (2003) suggested that infraspecific variation among *O. piliferum* isolates can be linked to geographic origin (North America versus Europe) or host (hardwoods versus conifers). The exact taxonomic status of these groups, and the synonymies listed above and discussed below thus should be reevaluated.

Ophiostoma capilliferum was considered a distinct species by Sydow & Sydow (1919), Melin & Nannfeldt (1934), Hunt (1956), and Käärik (1980). De Hoog (1974) could not locate ascospores or conidia on the type material of *O. capilliferum* (BPI) and considered the species doubtful. Upadhyay (1981), Hutchison & Reid (1988a) and Seifert *et al.* (1993) listed *O. capilliferum* as synonym of *O. piliferum*. *Ophiostoma schrenkianum* was also considered distinct species by Sydow & Sydow (1919), Melin & Nannfeldt (1934) and Hunt (1956). De Hoog (1974) found the teleomorph "indistinguishable from *O. piliferum*" on the type material (BPI), but because no conidia were found, he refrained from treating the two species as synonyms. Griffin (1968), Upadhyay (1981), Hutchison & Reid (1988a) and Seifert *et al.* (1993) listed *O. schrenkianum* as synonym of *O. piliferum*. *Ophiostoma coeruleum* was treated as a distinct species by Sydow & Sydow (1919), Lagerberg *et al.* (1927), Melin & Nannfeldt (1934) and Mathiesen-Käärik (1953). However, Goidánich (1936, 1937), Siemaszko (1939), Hunt (1956), Griffin (1968), Olchowecki & Reid (1974), de Hoog (1974), Upadhyay (1981), Hutchison & Reid (1988a) and Seifert *et al.* (1993) treated it as a synonym of *O. piliferum*.

Ophiostoma pluriannulatum (Hedgc.) Syd., *In* Sydow & Sydow, Annls mycol. 17: 43. 1919 ≡ *Ceratostomella pluriannulata* Hedgc., Mo. Bot. Gard. Ann. Rep. 17: 72. 1906 ≡ *Ceratocystis pluriannulata* (Hedgc.) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 = *Ceratocystis novae-zelandiae* Hutchison & J. Reid, N. Z. J. Bot. 26: 70. 1988 ≡ *Ophiostoma novae-zelandiae* (Hutchison & J. Reid) Rulamort, Bull. Soc. Bot. Centre-Ouest, n.s. 21: 512. 1990.

Anamorph: sporothrix-like.

Descriptions: Hedgcock (1906, pp 72–72, Pl. 3 Fig. 7, Pl. 5 Fig. 1–2); Lagerberg *et al*. (1927, pp 184–189, Figs 14–16); Hunt (1956, pp 15, 39–40); Upadhyay (1981, p. 109, Figs 387–392); Marmolejo & Butin (1993, pp 161, 169, Figs 28–32); Benade *et al.* (1998, pp 256–257, Figs 5–7).

Phylogenetic data: Hausner & Reid (2003); Thwaites *et al.* (2005); Villarreal *et al.* (2005); Zhou *et al.* (2006); Zipfel *et al.* (2006); Romón *et al.* (2007); Kamgan Nkuekam *et al.* (2008a, b); Linnakoski *et al*. (2009); Paciura *et al.* (2010b); Zanzot *et al*. (2010); De Beer & Wingfield (2012).

Note: *Ophiostoma pluriannulatum* is the oldest known and thus the name-bearing species of the *O. pluriannulatum* species complex in *Ophiostoma s.str.* (De Beer & Wingfield 2012). Griffin (1968) treated *O. pluriannulatum* as synonym of *O. piliferum*. The separation of the two species was confirmed in several of the phylogenetic studies cited above. Thwaites *et al.* (2005) suggested that the type material of *O. novae-zelandiae* was a mixture containing *O. pluriannulatum* and *O. piceae* or *O. quercus*. They showed that the available cultures of *O. novae-zelandiae* are sexually compatible with and have ITS sequences identical to those of *O. pluriannulatum*, and suggested the synonymy of the two species.

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

Anamorph: sporothrix-like.

Phylogenetic data: Hausner *et al.* (1993b).

Notes: This species groups close to *O. abietinum* according to Hausner *et al.* (1993b), but the LSU sequence they used is unavailable in GenBank, and could not be included in the larger phylogeny by De Beer & Wingfield (2012).

Ophiostoma populicola (Olchow. & J. Reid) Z.W. de Beer, Seifert, M.J. Wingf. ***comb. nov.,* MB 801090** ≡ *Ceratocystis populicola* Olchow. & J. Reid, Can. J. Bot. 52: 1700. 1974.

Anamorph: sporothrix-like.

Descriptions: Olchowecki & Reid (1974, p. 1700, Pl. X Figs 193–201); Upadhyay (1981, p. 57, Figs 153–157).

Notes: The new combination is based on sporothrix-like anamorph and morphology of ascospores, as described by Olchowecki & Reid (1974) and Upadhyay (1981). The name should not be confused with *Ceratocystis populicola* J.A. Johnson & T.C. Harr [*nom. illegit.*, Art. 53.1], see under *Ceratocystis harringtonii*.

Ophiostoma populinum (T.E. Hinds & R.W. Davidson) de Hoog & Scheffer, Mycologia 76: 297. 1984 ≡ *Ceratocystis populina* T.E. Hinds & R.W. Davidson, Mycologia 59: 1102. 1967.

Anamorph: sporothrix-like.

Description: Upadhyay (1981, p. 110, Figs 393–398).

Phylogenetic data: Hausner *et al.* (1993b); De Beer & Wingfield (2012).

Notes: LSU data place this species in the *O. pluriannulatum* complex. Thwaites *et al.* (2005) included two isolates with ITS sequences identical to *O. pluriannulatum*, but reproductively isolated from that species. They nevertheless suggested that these isolates might represent *O. populinum*.

Ophiostoma proliferum (Kowalski & Butin) Rulamort, Bull. Soc. Bot. Centre-Ouest, n.s. 21: 511. 1990 ≡ *Ceratocystis prolifera* Kowalski & Butin, J. Phytopathol. 124: 245. 1989.

Anamorph: sporothrix-like.

Notes: Cultural, anamorph and ascospore morphology all suggest placement of *O. proliferum* in the *S. schenckii – O. stenoceras* complex. However, annulations on the ascomatal necks resemble those present in species of the *O. pluriannulatum* complex.

Ophiostoma protearum G.J. Marais & M.J. Wingf., Can. J. Bot. 75: 363. 1997 = *Sporothrix protearum* G.J. Marais & M.J. Wingf., Can. J. Bot. 75: 364. 1997.

Anamorph: sporothrix-like.

Phylogenetic data: Viljoen *et al.* (1999); Wingfield *et al.* (1999); Roets *et al.* (2006, 2008, 2010, 2012); Zipfel *et al.* (2006); De Meyer *et al*. (2008); Harrington *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma protea-sedis Roets, M.J. Wingf. & Z.W. de Beer, Persoonia 24: 24. 2010.

Anamorph: sporothrix-like.

Phylogenetic data: Roets *et al*. (2010, 2012); De Beer & Wingfield (2012).

Notes: This species is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma pseudominus (Olchow. & J. Reid) Hausner, J. Reid & Klassen, Can. J. Bot. 71: 1264. 1993 ≡ *Ceratocystis pseudominor* Olchow. & J. Reid, Can. J. Bot. 52: 1708. 1974.

Anamorph: hyalorhinocladiella-like*.*

Description: Upadhyay (1981, p. 111, Figs 399–402).

Phylogenetic data: Hausner *et al.* (1993b); De Beer & Wingfield (2012).

Notes: The LSU sequence of *O. pseudominus* generated by Hausner *et al.* (1993b) differs only by one bp from that of *O. minus* (De Beer & Wingfield 2012).

Ophiostoma pseudonigrum (Olchow. & J. Reid) Hausner & J. Reid, Can. J. Bot. 81: 875. 2003 ≡ *Ceratocystis pseudonigra* Olchow. & J. Reid, Can. J. Bot. 52: 1693. 1974.

Anamorph: hyalorhinocladiella-like.

Phylogenetic data: Hausner & Reid (2003); Mullineux *et al*. (2011).

Notes: This specie was treated by Upadhyay (1981) as synonym of *O. nigrum*, but shown to be distinct by Hausner & Reid (2003). A short LSU sequence places this species in its own lineage in *Ophiostoma s. l.* (Hausner & Reid 2003; De Beer & Wingfield 2012). Ascospore and anamorph morphology resemble those of species of the *O. ips* complex, and therefore the phylogenetic placement of *O. pseudonigrum* should be explored further.

Ophiostoma pseudotsugae (Rumbold) Arx, Antonie van Leeuwenhoek 18: 211. 1952 ≡ *Ceratostomella pseudotsugae* Rumbold, J. Agric. Res. 52: 431. 1936 ≡ *Ceratocystis pseudotsugae* (Rumbold) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.

Anamorph: hyalorhinocladiella-like (Upadhyay 1981).

Phylogenetic data: Gorton & Webber (2000); Gorton *et al.* (2004); Linnakoski *et al.* (2008, 2010); Bommer *et al*. (2009); Lu *et al.* (2009a); De Beer & Wingfield (2012).

Notes: Hunt (1956) and Upadhyay (1981) both treated *O. pseudotsugae* as a synonym of *O. minus*, but Gorton & Webber (2000) and Gorton *et al.* (2004) later showed that *O. pseudotsugae* represents a distinct species, grouping close to *O. piliferum* (De Beer & Wingfield 2012).

Ophiostoma pulvinisporum X.D. Zhou & M.J. Wingf., Mycol. Res. 108: 694. 2004.

Anamorph: hyalorhinocladiella-like.

Phylogenetic data: Zhou *et al.* (2004b); Zipfel *et al.* (2006); Massoumi Alamouti *et al.* (2009); Linnakoski *et al.* (2010); Paciura *et al.* (2010b); Zanzot *et al*. (2010); De Beer & Wingfield (2012).

Notes: This species is part of the *O. ips* complex (De Beer & Wingfield 2012).

Ophiostoma pusillum Masuya, *In* Masuya *et al.*, Mycoscience 44: 302. 2003.
Anamorph: hyalorhinocladiella-like.
Note: *Ophiostoma pusillum* was described as morphologically similar to *O. nigrum* and *O. tubicolle* (Masuya *et al.* 2003a), and was treated by Masuya *et al*. (2012) in the *O. ips* complex based on morphology. However, the morphological similarity of *O. pusillum* with *O. nigrum* (Masuya *et al*. 2003) also suggests that this species might belong in *Graphilbum* (De Beer & Wingfield 2012). 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).

Ophiostoma quercus (Georgev.) Nannf., *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934 [as *'querci'* by some authors] ≡ *Ceratostomella quercus* Georgev., Compt. Rend. Hebd. Séances Acad. Sci. 183: 759. 1926 [as *'Querci'*] [*non Ceratostomella quercus* A.C. Santos & Sousa da Câmara, Agronomia Lusitania 17: 136. 1955, *nom. illegit.*, Art. 52.1] ≡ *Ceratocystis querci* (Georgev.) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 = *Ceratostomella fagi* W. Loos, Arch. Mikrobiol. 3: 376. 1932 ≡ *Ophiostoma fagi* (W. Loos) Nannf., *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934 ≡ *Ceratocystis fagi* (W. Loos) C. Moreau, Rev. Myc. (Paris) Suppl. Col. 17: 22. 1952 ≡ *Ceratocystis fagi* (W. Loos) Páclt, Česká Mykol. 8: 80. 1954 [*nom. illegit.*, Art. 52.1] = *Ophiostoma roboris* Georgescu & Teodoru, *In* Georgescu, Teodoru & Badea, Anal. Inst. Cerc. Exp. For. Rom., Ser 1. 11: 207. 1948 ≡ *Ceratocystis roboris* (Georgescu & Teodoru) Potl., *In* Potlajczuk & Schekunova, Nov. Sist. Niz. Rast. 22: 154. 1985 ≡ *Graphium roboris* Georgescu, Teodoru & Badea, Anal. Inst. Cerc. Exp. For. Rom., Ser 1. 11: 212. 1948 ≡ *Pesotum roboris* (Georgescu, Teodoru & Badea) Grobbelaar, Z.W. de Beer & M.J. Wingf., Mycol. Progress 8: 233. 2009 ≡ *Hyalodendron roboris* Georgescu & Teodoru, *In* Georgescu, Teodoru & Badea, Anal. Inst. Cerc. Exp. For. Rom., Ser 1. 11: 209. 1948 ≡ *Sporothrix roboris* (Georgescu & Teodoru) Grobbelaar, Z.W. de Beer & M.J. Wingf., Mycol. Progress 8: 233. 2009.
Synanamorphs: pesotum- and sporothrix-like.
Descriptions: Sczerbin-Parfenenko (1953, pp 47–49); Guseinov (1984, pp 145–148 as *O. roboris*); Potlajczuk & Schekunova (1985, pp 152–153 as *C. fagi*, and p. 154 as *C. roboris*); Halmschlager *et al.* (1994, pp 556–557); Harrington *et al.* (2001, pp 124–126); Grobbelaar *et al.* (2009, pp 226–233, Figs 1 & 2); Paciura *et al.* (2010b, pp 81–84, Figs 4, 8, 12, 15).
Phylogenetic data: Halmschlager *et al.* (1994); Kim *et al.* (1999, 2003, 2005a); Uzunovic *et al.* (2000); Harrington *et al.* (2001); Kim & Breuil (2001); Schroeder *et al.* (2001); De Beer *et al.* (2003d); Jacobs *et al.* (2003c); Jacobs & Kirisits (2003); Lin *et al.* (2003); Masuya *et al.* (2003b); Gebhardt *et al.* (2004); Geldenhuis *et al.* (2004); Zhou *et al.* (2004a, 2006); Thwaites *et al.* (2005); Villarreal *et al.* (2005); Carlier *et al.* (2006); Chung *et al.* (2006); Zipfel *et al.* (2006); Romón *et al.* (2007); Kamgan Nkuekam *et al.* (2008a, b, 2010); Linnakoski *et al.* (2008, 2009, 2010); Bommer *et al*. (2009); Grobbelaar *et al.* (2009, 2010, 2011); Massoumi Alamouti *et al.* (2009); Matsuda *et al.* (2010); Paciura *et al.* (2010b); Zanzot *et al*. (2010); Kim *et al.* (2011).
Note: *Ophiostoma quercus* forms part of the hardwood clade of the *O. piceae* complex (Harrington *et al*. 2001; Linnakoski *et al.* 2010), currently referred to as the *O. ulmi* complex (De Beer & Wingfield 2012). Hunt (1956), Griffin (1968), Olchowecki & Reid (1974), Upadhyay (1981), Hutchison & Reid (1988a), Kowalski & Butin (1989), and Przybyl & de Hoog (1989), all treated *O. quercus* as a synonym of *O. piceae*. Brasier & Webber (1990) suggested the separation of the two species, which was confirmed by several studies (Morelet 1992, Brasier & Kirk 1993, Brasier & Stephens 1993, Przybyl & Morelet 1993, Delatour *et al.* 1994, Halmschlager *et al.* 1994, Pipe *et al.* 1995, Kim *et al.* 1999, Harrington *et al.* 2001, De Beer *et al.* 2003c). Confusion exists in these publications regarding the correct formulation of the epithet (*'querci'* vs *'quercus'*). In a detailed argument, De Beer *et al.* (2003a) showed why *'quercus'* is the correct derivation.
Ophiostoma fagi was treated as of uncertain status by Hunt (1956), and as a synonym of *O. piceae* by de Hoog (1974), Upadhyay (1981), Hutchison & Reid (1988a) and Przybyl & de Hoog (1989). Harrington *et al.* (2001) and Grobbelaar *et al.* (2009) confirmed its synonymy

with *O. quercus* using sexual crosses and DNA sequence comparisons. *Ophiostoma roboris* was treated (along with *O. quercus*) as synonym of *O. piceae* by de Hoog (1979) and Kowalski & Butin (1989). Upadhyay (1981) excluded the species and Przybyl & de Hoog (1989) questioned the synonymy based on slight differences in anamorph morphology and a lack of authentic material. Brasier & Kirk (1989, 1993) successfully crossed an *O. roboris* isolate described by Guseinov (1984), with authentic *O. quercus* isolates, further suggesting it might be a synonym of *O. quercus*. In a four gene phylogeny, Grobbelaar *et al*. (2009) confirmed with that the Guseinov isolate and other *O. roboris*-like isolates from Azerbaijan represented *O. quercus*, and thus synonymized the two species.

The pesotum- and sporothrix-like synanamorphs of *O. quercus* were never supplied with binary names, while those of *O. roboris* were. When Grobbelaar *et al.* (2009) synonymized *O. roboris* with *O. quercus*, the binary names of *O. roboris* became available for application to the anamorphs of *O. quercus*, and new combinations were proposed. Under the Melbourne Code, these are now considered synonyms of *O. quercus*.

Ophiostoma rachisporum Linnakoski, Z.W. de Beer & M.J. Wingf., Persoonia 25: 83. 2010.

Anamorph: pesotum- and sporothrix-like.

Phylogenetic data: Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species groups in *Ophiostoma s. str.* (De Beer & Wingfield 2012).

Ophiostoma retusum (R.W. Davidson & T.E. Hinds) Hausner, J. Reid & Klassen, Mycol. Res. 97: 631. 1993 ≡ *Ceratocystis retusi* R.W. Davidson & T.E.Hinds, *In* Hinds & Davidson, Mycologia 64: 407. 1972 ≡ *Ceratocystiopsis retusi* (R.W. Davidson & T.E. Hinds) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 135. 1981.

Anamorph: sporothrix-like (Seifert *et al.* 1993, Benade *et al.* 1998).

Descriptions: Upadhyay (1981, p. 135, Figs 506–509); Benade *et al.* (1998, pp 258–259, Figs 8–11).

Phylogenetic data: Hausner *et al.* (1993a); Hausner & Reid (2003); Hafez *et al*. (2012); De Beer & Wingfield (2012).

Notes: *Ophiostoma retusum* is part of the *O. pluriannulatum* complex (De Beer & Wingfield 2012). See note under *O. carpenteri*.

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

Anamorph: sporothrix-like*.*

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

Phylogenetic data: Hausner *et al.* (1993b); Jacobs *et al.* (2003c); Villarreal *et al.* (2005); Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Note: *Ophiostoma rostrocoronatum* groups in the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012). Upadhyay (1981) listed Figs 399–402 as representing both *O. rostrocoronatum* and *Ceratocystis pseudominor.* The plate itself is labelled with the latter name, and Seifert *et al.* (1993) concluded that the former species was not illustrated.

Ophiostoma saponiodorum Linnakoski, Z.W. de Beer & M.J. Wingf., Persoonia 25: 88. 2010.

Synanamorphs: pesotum-like, hyalorhinocladiella-like.

Phylogenetic data: Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species groups with *O. pallidulum* in a distinct lineage within *Ophiostoma s.l.* (Linnakoski *et al*. 2010; De Beer & Wingfield 2012).

Sporothrix schenckii Hektoen & C.F. Perkins, J. Exp. Med. 5: 77. 1900 = *Sporotrichum beurmannii* Matr. & Ramond, Compt. Rend. Hebd. Séances Mém. Soc. Biol. 2: 380. 1905 ≡ *Sporotrichopsis beurmannii* (Matr. & Ramond) Gueguen, *In* De Beurmann & Gougerot, Archs Parasit. 15: 104. 1911 [*nom. inval*., Art. 34.1] ≡ *Sporothrix beurmannii* (Matr. & Ramond)

Meyer & Aird, J. Infect. Dis. 16: 399. 1915 ≡ for more homotypic synonyms of *S. beurmannii*, see de Hoog (1974, p. 37) = *Dolichoascus schenckii* Thibaut & Ansel, *In* Ansel & Thibaut, Compt. Rend. Hebd. Séances Acad. Sci. 270: 2173. 1970 [*nom. inval*., Art. 37.1].

For more synonyms of *S. schenckii*, see de Hoog (1974, pp 37–38).

Descriptions: De Beurmann & Gougerot (1911, pp 25–32, Figs 1–5, Plates I-V); de Hoog (1974, pp 36–44, Fig. 16); De Meyer *et al.* (2008, p. 655, Figs 4j-l); Matsushima (1975, p. 143, Plate 163).

Phylogenetic data: Berbee & Taylor (1992a, b); Marimon *et al.* (2007, 2008); De Meyer *et al.* (2008); Roets *et al*. (2008); Madrid *et al*. (2010); De Beer & Wingfield (2012).

Note: *Sporothrix schenckii* is the type species of *Sporothrix*, and groups with several other species in a distinct lineage, referred to as the *S. schenckii – O. stenoceras* complex, within *Ophiostoma s.l.* (De Beer & Wingfield 2012). For some years, *S. schenckii* was considered the anamorph of *O. stenoceras* (Taylor 1970, Mariat 1971, de Hoog 1974), but Summerbell *et al.* (1993) first suggested that the two species were distinct, later confirmed by De Beer *et al.* (2003b) using ITS sequences. No teleomorph is currently known for *S. schenckii*. Several recent phylogenetic studies of *S. schenckii* show that the human and animal pathogens form several closely related lineages (Marimon *et al.* 2007). Three lineages are already described as distinct species, namely *S. brasiliensis*, *S. globosa*, and *S. luriei* (Marimon *et al*. 2007, 2008). The status of the other lineages remains to be clarified.

Several synonyms for *S. schenckii*, all originating from the medical literature predating 1940, are listed by de Hoog (1974) and in MYCOBANK. We did not list these here, except for *S. beurmannii* and *D. schenckii* for the reasons discussed below. *Sporothrix beurmannii* is the type species of *Sporotrichopsis* Guég., published only as a provisional name (De Beurmann & Gougerot 1911) and that is invalid (Art. 34.1). The generic name is now occupied by *Sporotrichopsis* Stalpers. Davis (1920) convincingly argued that *S. beurmannii* is a synonym of *S. schenckii*, a suggestion followed by de Hoog (1974), which implies that *Sporotrichopsis*, had it been valid, would be a synonym of *Sporothrix*. *Dolichoascus schenckii* is the type of *Dolichoascus*, but that species, and thus the genus as well, was invalidly published (Ansel & Thibaut 1970) because a holotype was not indicated [Art. 34.1]. Ansel & Thibaut (1970) and Thibaut (1972) described endogenous ascospores, and suggested *Dolichoascus* (*Endomycetaceae*) was the teleomorph of *S. schenckii*. Mariat & Diez (1971) studied the strain (CBS 938.72) of Ansel & Thibaut (1970) and argued that the ‘ascospores’ were actually endoconidia. According to de Hoog (1974), the name *Dolichoascus* could thus not be used for an anamorph genus. However, the *D. schenckii* isolate is still viable and therefore lectotypifcation (Art. 90.2) and validation of the species and genus would be possible. Furthermore, the Mebourne Code allows the use of *Dolichoascus* whether a teleomorph is present or not. However, Marimon *et al.* (2007) produced a calmodulin sequence for the *D. schenckii* isolate which placed it among *S. schenckii* isolates. Despite this, there is no need for lectotypification or validation of *Dolichoascus.* because it would only become a synonym of *Sporothrix*.

The remaining synonyms for *S. schenckii* should all be re-considered in future studies delimiting phylogenetic species in this large complex.

Ophiostoma sejunctum M. Villarreal, Arenal, V. Rubio & M. de Troya, *In* Villarreal *et al.*, Mycotaxon 92: 260. 2005.

Anamorph: hyalorhinocladiella-like.

Phylogenetic data: Villarreal *et al.* (2005); De Beer & Wingfield (2012).

Notes: This species groups with *O. angusticollis* in a distinct lineage close to the *O. tenellum* complex (De Beer & Wingfield 2012).

Ophiostoma setosum Uzunovic, Seifert, S.H. Kim & C. Breuil, Mycol. Res. 104: 490. 2000.

Anamorph: pesotum- and sporothrix-like.

Descriptions: Harrington *et al.* (2001, pp 121, 123–124); Paciura *et al.* (2010b, p. 84, Figs 6, 10, 14, 17).

Phylogenetic data: Uzunovic *et al.* (2000); Harrington *et al.* (2001); Schroeder *et al.* (2001); Jacobs *et al.* (2003c); Jacobs & Kirisits (2003); Masuya *et al.* (2003b); Kim *et al.* (2005a); Carlier *et al.* (2006); Chung *et al.* (2006); Kamgan Nkuekam *et al.* (2008b, 2010); Linnakoski *et al.* (2008, 2009, 2010); Bommer *et al*. (2009); Lu *et al.* (2009a, b); Massoumi Alamouti *et al.* (2009); Grobbelaar *et al*. (2010, 2011); Paciura *et al.* (2010b); Zanzot *et al*. (2010); (De Beer & Wingfield 2012).

Notes: Harrington *et al.* (2001) described *P. cupulatum* as the anamorph of *O. setosum* based on mating compatibility, but did not include sequences of the ex-type of *O. setoum* in their analyses. ITS sequences of the ex-types of *O. setosum* (Uzunovic *et al.* 2000) and *P. cupulatum* differ by 12 bp (De Beer & Wingfield 2012). We thus consider the two species distinct.

Ophiostoma sparsiannulatum Zanzot, Z.W. de Beer & M.J. Wingf., Mycol. Progress 9: 452. 2010.

Anamorph: sporothrix-like.

Phylogenetic data: Zanzot *et al.* (2010); De Beer & Wingfield (2012).

Notes: ITS sequences of *O. sparsiannulatum* are identical to those of *O. pluriannulatum*, but the species have very different β-tubulin sequences (Zanzot *et al.* 2010; De Beer & Wingfield 2012). It is part of the *O. pluriannulatum* complex (De Beer & Wingfield 2012).

Ophiostoma spinosum P. Cannon, Syst. Ascomycet. 15: 127. 1997.

Anamorph: Not observed.

Note: *Ophiostoma spinosum* is characterized by relatively short *Ceratocystiopsis*-like ascomata, with pigmented setae surrounding the ostiole, and short bacilliform ascospores lacking sheaths (Cannon 1997). These unique characters and the lack of a known anamorph or a living culture, prevents an accurate placement of the species within the *Ophiostomatales*. The name should not be confused with *Ophiostoma spinosum* Willemoes-Suhm, a parasitic nematode, or *Ceratocystis spinosa* Ubaghs, an invertebrate fossil (Table 1).

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

Anamorph: sporothrix-like.

Description: Marais & Wingfield (2001, pp 243–246).

Phylogenetic data: Viljoen *et al.* (1999); Wingfield *et al.* (1999); Roets *et al.* (2006, 2008, 2010); Zipfel *et al.* (2006); De Meyer *et al*. (2008); Harrington *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma ssiori Masuya, Kubono & Ichihara, Bull. Nat. Sci. Mus., Tokyo, Ser. B 29: 39. 2003.

Synanamorphs: pesotum- and sporothrix-like*.*

Phylogenetic data: Masuya *et al.* (2003b); Villarreal *et al.* (2005); Linnakoski *et al.* (2008); Kamgan Nkuekam *et al.* (2010); De Beer & Wingfield (2012).

Notes: *Ophiostoma ssiori* groups close to *O. subalpinum* in *Ophiostoma s. str.* (De Beer & Wingfield 2012).

Ophiostoma stenoceras (Robak) Nannf., *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934 ≡ *Ceratostomella stenoceras* Robak, Nyt Mag. Naturvid. Oslo 71: 214. 1932 ≡ *Ceratocystis stenoceras* (Robak) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 = *Ophiostoma albidum* Math.-Käärik, Medd. Skogsforskninginst. 43: 52. 1953 ≡ *Ceratocystis albida* (Math.-Käärik) J. Hunt, Lloydia 19: 48. 1956 = *Ceratocystis gossypina var. robusta* R.W. Davidson, Mycologia 63: 13. 1971 = *Ceratocystis ponderosae* T.E. Hinds & R.W. Davidson, Mycologia 67: 715. 1975 ≡ *Ophiostoma ponderosae* (T.E. Hinds & R.W. Davidson)

Hausner, J. Reid & Klassen, Can. J. Bot. 71: 1264. 1993 = *Ceratocystis eucastaneae* R.W. Davidson, Mycologia 70: 856. 1978.

Anamorph: sporothrix-like.

Descriptions: Davidson (1942, pp 651–655); Griffin (1968, p. 713, Fig. 83, 90, Pl. I, III); de Hoog (1974, pp 36–44); Olchowecki & Reid (1974, p. 1709); Upadhyay (1981, p. 113, Figs 403–407); Kowalski & Butin (1989, pp 242–243).

Phylogenetic data: Berbee & Taylor (1992a, b); Okada *et al.* (1998); Hausner *et al.* (2000); De Beer *et al.* (2003b); Hausner & Reid (2003); Jacobs *et al.* (2003c); Aghayeva *et al.* (2004, 2005); Zhou *et al.* (2004b, 2006); Gebhardt *et al.* (2005)*;* Thwaites *et al.* (2005); Villarreal *et al.* (2005); Roets *et al.* (2006, 2008, 2010); Zipfel *et al.* (2006); Romón *et al.* (2007); De Meyer *et al*. (2008); Linnakoski *et al*. (2009); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Madrid *et al*. (2010); Paciura *et al.* (2010b); Kim *et al.* (2011).

Note: The anamorph of *O. stenoceras* has often been referred to as *S. schenckii*, but the two species are distinct (see under *S. schenckii*), forming the core of the *S. schenckii – O. stenoceras* complex (De Beer *et al.* 2003d; De Beer & Wingfield 2012).

Ophiostoma albidum was treated as a distinct species by Hunt (1956), Griffin (1968), and Olchowecki & Reid (1974). De Hoog (1974), Upadhyay (1981) and Seifert *et al.* (1993) treated it as synonym of *O. stenoceras*. Hausner & Reid (2003) and De Beer *et al.* (2003b) respectively showed that LSU and ITS sequences of *O. albidum* are identical to those of *O. stenoceras*, supporting the synonymy of the two species.

The distinction between *O. gossypinum* and *C. gossypina var. robusta* by Davidson (1971) was based only on perithecium morphology. Subsequent authors treated both species as synonyms of *O. stenoceras* (Upadhyay 1981, Seifert *et al.* 1993). Hausner & Reid (2003) showed that *O. gossypinum* is distinct from *O. stenoceras*, while Villarreal (2005) showed the ITS sequence of the ex-type isolate of *C. gossypina var. robusta* to be identical to that of *O. stenoceras*.

De Beer *et al.* (2003b) showed that the ex-type of *O. ponderosae* (ATCC 26665 = RWD 900) has an identical ITS sequence to *O. stenoceras*. An LSU sequence produced by Hausner *et al.* (1993b, not in GenBank) of another *O. ponderosae* isolate (CBS 496.77 = RWD 899,) from the study of Hinds and Davidson (1975), groups in the *O. pluriannulatum* complex, but we accept the synonymy with *O. stenoceras* by De Beer *et al.* (2003b) based on the ex-type.

Ceratocystis eucastanea was suggested as a synonym of *O. stenoceras* by Upadhyay (1981), and this was accepted by Seifert *et al.* (1993).

Sporothrix stylites de Mey., Z.W. de Beer & M.J. Wingf., Mycologia 100: 656. 2008.

Description: De Meyer *et al.* (2008, p. 656, Figs 4a–c).

Phylogenetic data: De Meyer *et al.* (2008); Madrid *et al*. (2010); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma subalpinum Ohtaka & Masuya, *In* Ohtaka *et al.*, Mycoscience 43: 152. 2002.

Anamorph: pesotum-like.

Phylogenetic data: Masuya *et al.* (2003b); Villarreal *et al.* (2005); Chung *et al.* (2006); Bommer *et al*. (2009); Linnakoski *et al*. (2009); Lu *et al.* (2009a); Kamgan Nkuekam *et al.* (2010); Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species is part of *Ophiostoma s.str.* (De Beer & Wingfield 2012).

Ophiostoma subannulatum Livingston & R.W. Davidson, Mycologia 79: 145. 1987 = *Sporothrix subannulata* Livingston & R.W. Davidson, Mycologia 79: 145. 1987.

Anamorph: sporothrix-like.

Phylogenetic data: Hausner & Reid (2003); Villarreal *et al.* (2005); Zipfel *et al.* (2006); Kamgan Nkuekam *et al.* (2008a, b); Linnakoski *et al*. (2009); Paciura *et al.* (2010b); Zanzot *et al*. (2010); De Beer & Wingfield (2012).

Notes: *Ophiostoma subannulatum* is part of the *O. pluriannulatum* complex (Zanzot *et al.* 2010; De Beer & Wingfield 2012).

Ophiostoma tapionis Linnakoski, Z.W. de Beer & M.J. Wingf., Persoonia 25: 84. 2010.
Anamorph: hyalorhinocladiella-like.
Phylogenetic data: Linnakoski *et al.* (2010); De Beer & Wingfield (2012).
Notes: A species known only by its anamorph. Groups with *O. brunneo-ciliatum* and *O. ainoae*, close to *O. floccosum* in *Ophiostoma* s.str. (De Beer & Wingfield 2012).

Ophiostoma tasmaniense Kamgan, Jol. Roux & Z.W. de Beer, *In* Kamgan Nkuekam *et al*., Austral. J. Bot. 59: 291. 2011.
Anamorph: pesotum-like.
Phylogenetic data: Kamgan Nkuekam *et al.* (2011); De Beer & Wingfield (2012).
Notes: This species is part of the *O. ulmi* complex (Kamgan Nkuekam *et al.* 2011; De Beer & Wingfield 2012).

Ophiostoma tenellum (R.W. Davidson) M. Villarreal, Mycotaxon 92: 263. 2005 ≡ *Ceratocystis tenella* R.W. Davidson, Mycologia 50: 666. 1958 = *Ceratocystis capitata* H.D. Griffin, Can. J. Bot. 46: 699. 1968.
Anamorph: sporothrix-like.
Descriptions: Griffin (1968, pp 713, 715, Fig. 93 Pl. III); Olchowecki & Reid (1974, p. 1708, Pl. XVI Figs 307–308, 311–312); Upadhyay (1981, p. 114, Figs 408–412); Maekawa *et al.* (1987, pp 10–11, Figs 19–20); Hutchison & Reid (1988a, p. 68).
Phylogenetic data: Villarreal *et al.* (2005); Linnakoski *et al.* (2010); De Beer & Wingfield (2012).
Note: *Ophiostoma tenellum* groups together with *O. nigricarpum* and *O. coronatum* in a distinct lineage peripheral to the *S. schenckii – O. stenoceras* complex (Linnakoski *et al.* 2010; De Beer & Wingfield 2012). *Ceratocystis capitata* was treated as a distinct species by Olchowecki and Reid (1974), but as a synonym of *O. tenellum* by Upadhyay (1981) and Villarreal *et al.* (2005).

Ophiostoma tetropii Math., Svensk. Bot. Tidskr. 45: 228. 1951 ≡ *Ceratocystis tetropii* (Math.) J. Hunt, Lloydia 19: 45. 1956.
Anamorph: leptographium- to hyalorhinocladiella-like (Jacobs *et al.* 2003c; Jacobs & Seifert 2004).
Descriptions: Mathiesen (1950, p. 301); Hunt (1956, pp 11, 15, 45); Kotýnková-Sychrová (1966, p. 52); de Hoog (1974, p. 45); Olchowecki & Reid (1974, p. 1709); Upadhyay (1981, p. 115, Figs 413–417); Solheim (1986, p. 206); Jacobs *et al.* (2003c, pp 323–326, Figs 7–21); Jacobs & Seifert (2004, pp 76–77, Figs 1–7).
Phylogenetic data: Hausner *et al.* (1993b, 2000); Jacobs *et al.* (2003a); Jacobs & Kirisits (2003); Masuya *et al.* (2004); Villarreal *et al.* (2005); Carlier *et al.* (2006); Kamgan Nkuekam *et al.* (2008b, 2010); Linnakoski *et al.* (2008, 2010); Bommer *et al*. (2009); De Beer & Wingfield (2012).
Notes: Jacobs *et al.* (2003c) clarified the confusion surrounding the atypical ex-type culture of *O. tetropii* and designated both a lectotype and an epitype for the species. Linnakoski *et al*. (2010) treated *O. tetropii* as part of the *O. minus* complex, but in the analyses of De Beer & Wingfield (2012), the species is placed separately from *O. minus* in *Ophiostoma s.str.*

Ophiostoma tingens (Lagerb. & Melin) Z.W. de Beer & M.J. Wingf. ***comb. nov.,* MB 801091** ≡ *Trichosporum tingens* Lagerb. & Melin, *In* Lagerberg *et al.*, Svenska SkogsvFör. Tidskr. 25: 238. 1927 (basionym) [as *'Trichosporium tingens*'] (basionym) ≡ *Ambrosiella tingens* (Lagerb. & Melin) L.R. Batra, Mycologia 59: 980. 1967 ≡ *Hyalorhinocladiella tingens* (Lagerb. & Melin) T.C. Harr., *In* Harrington *et al.*, Mycotaxon 111: 356. 2010.
Anamorph: hyalorhinocladiella- to raffaelea-like.

Description: Lagerberg *et al.* (1927, pp 233–238, Figs 43–47).

Phylogenetic data: Rollins *et al.* (2001); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species forms a distinct lineage together with *O. macrosporum* in *Ophiostoma s.str.* (De Beer & Wingfield 2012). The arguments for the new combination are presented under Lineage B in De Beer & Wingfield (2012).

Ophiostoma torticiliata (Olchow. & J. Reid) Seifert & G. Okada, *In* Okada *et al.*, Can. J. Bot. 76: 1504. 1998 ≡ *Ceratocystis torticiliata* Olchow. & J. Reid, Can. J. Bot. 52: 1701. 1974.

Anamorph: pesotum-like (Okada *et al.* 1998).

Descriptions: Olchowecki & Reid (1974, pp 1701–1702, Pl. XII Figs 239–250); Upadhyay (1981, p. 61, Figs 172–177); Seifert & Okada (1993, p. 33, Fig. 4B).

Notes: *Ophiostoma torticiliata* is morphologically similar to *O. clavatum* (Olchowecki & Reid 1974). Its sheathed ascospores suggest a possible relationship with *Grosmannia*.

Ophiostoma torulosum (Butin & G. Zimm.) Hausner, J. Reid & Klassen, Can. J. Bot. 71: 1264. 1993 ≡ *Ceratocystis torulosa* Butin & G. Zimm., Phytopathol. Z. 74: 284. 1972.

Anamorph: sporothrix- to hyalorhinocladiella-like.

Phylogenetic data: Hausner *et al.* (1993b, 2000); Gebhardt *et al.* (2004); Masuya *et al.* (2004); De Beer *et al*. (2012); De Beer & Wingfield (2012).

Notes: Treated as synonym of *O. distortum* by Upadhyay (1981), but Hausner *et al*. (1993b) showed that *O. torulosum* is distinct. It groups near *O. ulmi* based on SSU (De Beer *et al*. 2012) and LSU data (De Beer & Wingfield 2012). Its position in the *O. ulmi* complex needs confirmation with ITS data because it does not produce a synnematous anamorph, characteristic of all other species in the complex.

Ophiostoma tremulo-aureum (R.W. Davidson & T.E. Hinds) de Hoog & Scheffer, Mycologia 76: 298. 1984 ≡ *Ceratocystis tremulo-aurea* R.W. Davidson & T.E. Hinds, *In* Davidson, Hinds & Toole, Mycologia 56: 794. 1964.

Anamorph: hyalorhinocladiella-like (Upadhyay 1981).

Descriptions: Olchowecki & Reid (1974, p. 1709, Pl. XVI Fig. 317); Upadhyay (1981, p. 115, Figs 418–421).

Phylogenetic data: Hausner & Reid (2003); De Beer *et al*. (2012); De Beer & Wingfield (2012).

Notes: The LSU sequence of the ex-type isolate (CBS 361.65) produced by Hausner & Reid (2003) places *O. tremulo-aureum* in the *O. ips* complex (De Beer & Wingfield 2012). However, the ascospore shape and hardwood origin of this species suggest a placement in the *O. ulmi* complex. A careful re-assessment of the ex-type culture and additional material is needed to confirm the placement in this species complex.

Ophiostoma triangulosporum Butin, Phytopathol. Z. 91: 230. 1978 ≡ *Ceratocystis triangulospora* (Butin) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 62. 1981.

Anamorph: raffaelea- to hyalorhinocladiella-like (Butin 1978, Upadhyay 1981).

Description: Upadhyay (1981, p. 62, Figs 178–184).

Phylogenetic data: Hausner & Reid (2003); Villarreal *et al.* (2005); Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species is peripheral to the *O. ulmi* complex (De Beer & Wingfield 2012). This relationship needs confirmation with more sequences because ascospores of this species have unique, triangular sheaths, different from other species in the *O. ulmi* complex (De Beer & Wingfield 2012).

Ophiostoma tsotsi Grobbelaar, Z.W. de Beer & M.J. Wingf., Mycopathologia 169: 419. 2010.

Synanamorphs: pesotum- and sporothrix-like.

Phylogenetic data: Grobbelaar *et al*. (2010, 2011); Linnakoski *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species is part of the *O. ulmi* complex (De Beer & Wingfield 2012).

Ophiostoma ulmi (Buisman) Nannf., *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934 ≡ *Ceratostomella ulmi* Buisman, Tijdskr. Plantenziekt. 38: 1. 1932 ≡ *Ceratocystis ulmi* (Buisman) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 = *Graphium ulmi* M.B. Schwarz, Meded. Phytopathol. Lab. 5: 10. 1922 ≡ *Pesotum ulmi* (M.B. Schwarz) Crane & Schoknecht, Am. J. Bot. 60: 348. 1973.

Synanamorphs: pesotum- and sporothrix-like (de Hoog 1974).

Descriptions: Schwarz (1928, English translation of original, German description of *Gr. ulmi*); Siemaszko (1939, pp 36–37, Pl. V Figs 8–9); Hunt (1956, pp 38–39); Griffin (1968, pp 715–716, Fig. 84 Pl. I); Booth & Gibson (1973, pp 1–2, Figs A-F); Olchowecki & Reid (1974, p. 1709*)*; de Hoog (1974, pp 50–53, Fig. 19); Upadhyay (1981, p. 117, Figs 422–427); Potlajczuk & Schekunova (1985, p. 155); Harrington *et al.* (2001, pp 126–127). Of pesotum-like anamorph: Crane & Schoknecht (1973, pp 347–348, Figs 1–13); Mouton *et al.* (1993, pp 372–375, Figs 5–8, 13); Seifert & Okada (1993, p. 33, Fig. 4A).

Phylogenetic data: Berbee & Taylor (1992a, b); Bates *et al.* (1993a, b); Hausner *et al.* (1993b, 2000); Jeng *et al.* (1996); Brasier *et al.* (1998); Okada *et al.* (1998); Harrington *et al.* (2001); Schroeder *et al.* (2001); Hausner & Reid (2003); Jacobs *et al.* (2003c); Jacobs & Kirisits (2003); Masuya *et al.* (2003b, 2004); Gebhardt *et al.* (2005)*;* Gibb & Hausner (2005); Paoletti *et al.* (2005); Villarreal *et al.* (2005); Carlier *et al.* (2006); Zipfel *et al.* (2006); Tang *et al.* (2007); Kamgan Nkuekam *et al.* (2008a, b, 2010); Linnakoski *et al.* (2008); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); Paciura *et al.* (2010b); De Beer & Wingfield (2012).

Notes: *Pesotum ulmi* is the type species of *Pesotum* (Crane & Schoknecht 1973), currently treated as synonym of *Ophiostoma*. *Ophiostoma ulmi* is the oldest and thus nominal species of the *O. ulmi* complex (De Beer & Wingfield 2012).

Ophiostoma undulatum Kamgan, Jol. Roux & Z.W. de Beer, *In* Kamgan Nkuekam *et al*., Austral. J. Bot. 59: 291. 2011.

Anamorph: sporothrix-like.

Phylogenetic data: Kamgan Nkuekam *et al.* (2011).

Notes: This species is part of the *O. ulmi* complex (Kamgan Nkuekam *et al.* 2011, De Beer & Wingfield 2012).

Ophiostoma valachicum Georgescu, Teodoru & Badea, Anal. Inst. Cerc. Exp. For. Rom., Ser 1. 11: 198. 1948 ≡ *Rhinotrichum valachicum* Georgescu, Teodoru & Badea, Anal. Inst Cerc. Exp. For., Ser. 1, 11: 201. 1948 ≡ *Ceratocystis valachicum* (Georgescu, Teodoru & Badea) Potl., *In* Potlajczuk & Schekunova, Nov. Sist. Niz. Rast. 22: 155. 1985.

Anamorph: sporothrix-like (Przybyl & de Hoog 1989).

Descriptions: Sczerbin-Parfenenko (1953, pp 47–48); Potlajczuk & Schekunova (1985, p. 155).

Notes: *Ophiostoma valachicum* was treated as a *nomen dubium* by Upadhyay (1981), while others considered it a possible synonym of *O. piceae* (Przybyl & de Hoog 1989) or *O. quercus* (Harrington *et al.* 2001)*.* Authentic material was unavailable for these studies. Georgescu *et al.* (1948) mentioned only a sporothrix-like anamorph (as *Rhinotrichum*). Sczerbin-Parfenenko (1953) also stated that no other anamorphs are known. Grobbelaar *et al*. (2009) suggested that the confusion with *O. piceae* originated from Potlajczuk & Schekunova (1985) who mentioned, but did not describe, a *Graphium* state. However, they also described the ascospores as ‘a little curved’, while Georgescu *et al.* (1948) and Sczerbin-Parfenenko (1953) described and illustrated the ascospores as *semilunarii* and crescent-shaped, respectively. Therefore, it seems likely that the material described by Potlajczuk & Schekunova (1985) did not represent *O. valachicum*. For these reasons, Grobbelaar *et al*. (2009) concluded that although no material is currently available for this species, it is distinct. Recollection followed by neotypification (Art. 9.6) are prerequisites for determining the correct phylogenetic placement of the species.

Sporothrix variecibatus Roets, Z.W. de Beer & Crous, Mycologia 100: 506. 2008.
Description: Roets (2008, p. 506, Fig. 6).
Phylogenetic data: Roets *et al*. (2008, 2010, 2012); De Beer & Wingfield (2012).
Notes: Teleomorph unknown. This species belongs to the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ophiostoma zambiensis Roets, M.J. Wingf. & Z.W. de Beer, Persoonia 24: 24. 2010.
Anamorph: sporothrix-like.
Phylogenetic data: Roets *et al*. (2010, 2012); De Beer & Wingfield (2012).
Notes: This species groups with other *Protea*-infesting species of the *S. schenckii – O. stenoceras* complex (De Beer & Wingfield 2012).

Ceratocystiopsis H.P. Upadhyay & W.B. Kendr., Mycologia 67: 799. 1975. emend. Z.W. de Beer, Zipfel & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 87. 2006 [type species *Cop. minuta*]
= *Hyalorhinocladiella* H.P. Upadhyay & W.B. Kendr., Mycologia 67: 800. 1975. Anamorphic synonym. [type species *Cop. minuta-bicolor*]
Notes: For adiscussion of this genus, see De Beer *et al*. (2012) and De Beer & Wingfield (2012). The anamorph of *Cop. minuta-bicolor* is the type of *Hyalorhinocladiella*; the species groups within *Ceratocystiopsis* (De Beer & Wingfield 2012), rendering *Hyalorhinocladiella* a synonym of *Ceratocystiopsis*.

Ceratocystiopsis brevicomis Hsiau & T.C. Harr., Mycologia 89: 662. 1997.
Anamorph: sporothrix-like.
Phylogenetic data: Hsiau & Harrington (1997); Six & Paine (1999); Plattner *et al.* (2009); Hafez *et al*. (2012); De Beer & Wingfield (2012).

Ceratocystiopsis collifera Marm. & Butin, Sydowia 42: 197. 1990 ≡ *Ophiostoma colliferum* (Marm. & Butin) Hausner, J. Reid & Klassen, Mycol. Res. 97: 631. 1993 [as *'coliferum'*]
Anamorph: sporothrix-like.
Description: Marmolejo & Butin (1993, pp 162, 169, Figs 33–37).
Phylogenetic data: Hausner *et al.* (1993a, 2000); Hausner & Reid (2003); Mullineux & Hausner (2009); Plattner *et al.* (2009); Hafez *et al*. (2012); De Beer & Wingfield (2012).
Notes: LSU data place *Cop. collifera* in *Ceratocystiopsis* (Hausner *et al*. 1993a, Plattner *et al.* 2009), but published ITS and β-tubulin data of the same isolate (Plattner *et al.* 2009) correspond closely with those of *O. abietinum* in *S. schenckii – O. stenoceras* complex. We suggest careful reconsideration of the ex-type strain (CBS 126.89) to confirm these unlikely results, which might be the result of a mixed culture.

Ceratocystiopsis concentrica (Olchow. & J. Reid) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 121. 1981 ≡ *Ceratocystis concentrica* Olchow. & J. Reid, Can. J. Bot. 52: 1679. 1974 ≡ *Ophiostoma concentricum* (Olchow. & J. Reid) Hausner & J. Reid, Can. J. Bot. 81: 874. 2003.
Anamorph: hyalorhinocladiella-like (de Hoog 1993).
Description: Upadhyay (1981, p. 121, Figs 432–435).
Phylogenetic data: Réblová & Winka (2000); Hausner & Reid (2003); Hafez *et al*. (2012); De Beer & Wingfield (2012).

Ceratocystiopsis conicicollis (Olchow. & J. Reid) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 122. 1981 ≡ *Ceratocystis conicicollis* Olchow. & J. Reid, Can. J. Bot. 52: 1680. 1974.

Anamorph: hyalorhinocladiella-like (Upadhyay 1981).

Description: Upadhyay (1981, p. 122, Figs 436–439).

Ceratocystiopsis longispora (Olchow. & J. Reid) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 128. 1981 ≡ *Ceratocystis longispora* Olchow. & J. Reid, Can. J. Bot. 52: 1683. 1974 ≡ *Ophiostoma longisporum* (Olchow. & J. Reid) Hausner, J. Reid & Klassen, Mycol. Res. 97: 631. 1993.

Anamorph: hyalorhinocladiella- to sporothrix-like*.*

Descriptions: Olchowecki & Reid (1974, pp 1683–1684, Pl. IV Figs 65–73); Upadhyay (1981, p. 128, Figs 466–471).

Phylogenetic data: Hausner *et al.* (1993a); Hausner & Reid (2003); Plattner *et al*. (2009); Hafez *et al*. (2012); De Beer & Wingfield (2012).

Notes: The morphology of *O. longisporum*, especially the falcate ascospores, resembles other *Ceratocystiopsis* species. DNA sequences suggest this species is slightly distinct from, but always in a monophyletic lineage with significant support values. together with other species of *Ceratocystiopsis* (Hausner *et al*. 1993a; Hausner & Reid 2003; Plattner *et al*. 2009; Hafez *et al*. 2012; De Beer & Wingfield 2012), confirming the classification suggested by Upadhyay (1981).

Ceratocystiopsis manitobensis (J. Reid & Hausner) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 87. 2006 ≡ *Ophiostoma manitobense* J. Reid & Hausner, *In* Hausner *et al.*, Can. J. Bot. 81: 46. 2003.

Anamorph: hyalorhinocladiella-like.

Phylogenetic data: Hausner *et al.* (1993a) (as '*Ceratocystiopsis* sp. 3'); Zipfel *et al.* (2006); Massoumi-Alamouti *et al.* (2007, 2009); Plattner *et al.* (2009); Hafez *et al*. (2012); De Beer & Wingfield (2012).

Notes: Phylogenetic analyses by Plattner *et al.* (2009) show two lineages within *Cop. manitobensis*, possibly representing distinct taxa and worthy of further exploration.

Ceratocystiopsis minima (Olchow. & J. Reid) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 129. 1981 ≡ *Ceratocystis minima* Olchow. & J. Reid, Can. J. Bot. 52: 1684. 1974 ≡ *Ophiostoma minimum* (Olchow. & J. Reid) Hausner, J. Reid & Klassen, Mycol. Res. 97: 631. 1993.

Anamorph: hyalorhinocladiella-like (Upadhyay 1981).

Description: Upadhyay (1981, p. 129, Figs 472–482).

Phylogenetic data: Hausner *et al.* (1993a); Hausner & Reid (2003); Zipfel *et al.* (2006); Plattner *et al.* (2009); Hafez *et al*. (2012); De Beer & Wingfield (2012).

Ceratocystiopsis minuta (Siemaszko) H.P. Upadhyay & W.B. Kendr., Mycologia 67: 800. 1975 ≡ *Ophiostoma minutum* Siemaszko, Planta Pol. 7: 23. 1939 ≡ *Ceratostomella minuta* (Siemaszko) R.W. Davidson, Mycologia 34: 655. 1942 ≡ *Ceratocystis minuta* (Siemaszko) J. Hunt, Lloydia 19: 49. 1956 = *Ceratocystis dolominuta* H.D. Griffin, Can. J. Bot. 46: 702. 1968.

Anamorph: hyalorhinocladiella-like (Upadhyay 1981).

Descriptions: Davidson (1942, pp 655–657); Mathiesen (1951, pp 205–208); Hunt (1956, pp 11, 49); Kotýnková-Sychrová (1966, p. 52); Griffin (1968, pp 702–703; Fig. 80 Pl. I); Olchowecki & Reid (1974, p. 1685); Upadhyay (1981, p. 130, Figs 483–494); Marmolejo & Butin (1993, pp 163, 170, Figs 42–43); Yamaoka *et al.* (1997, pp 1216–1217); Yamaoka *et al.* (1998, Figs 2–5, p. 369).

Phylogenetic data: Hausner *et al.* (1993a, c, 2000); Hausner & Reid (2003); Zipfel *et al.* (2006); Massoumi-Alamouti *et al.* (2007, 2009); Plattner *et al*. (2009); Hafez *et al*. (2012); De Beer *et al*. (2012); De Beer & Wingfield (2012).

Note: Plattner *et al.* (2009) showed that 23 putative isolates of *Cop. minuta* of diverse origins grouped in seven lineages, two including new isolates from Poland from where *Cop. minuta* was initially described. The lack of type material prevented them from designating one of these two lineages as *Cop. minuta sensu stricto*. Reid & Hausner (2010) proceeded to designate one of the new Polish isolates as epitype. The remaining '*Cop. minuta*' lineages, distinguished by Plattner *et al.* (2009) referred to as *Cop. minuta* sp. 1 and sp. 2 by De Beer & Wingfield (2012), thus should be described as novel taxa.

Griffin (1968) was unable to obtain living cultures for *C. dolominuta* and described only the teleomorph of this species. Olchowecki & Reid (1974) later obtained cultures and described the anamorph (p. 1682, Figs 17–19). Upadhyay (1981) suggested that *C. dolominuta* should be a synonym of *Cop. minuta* based on overlapping ascospore lengths. Reid & Hausner (2010) disputed the synonymy because *C. dolominuta* consistently produces shorter ascospores than *Cop. minuta.* Epitypification and DNA sequence data will resolve the uncertain status of the species. Should it prove to be distinct, a new combination should be provided for *C. dolominuta* in *Ceratocystiopsis*.

Ceratocystiopsis minuta-bicolor (R.W. Davidson) H.P. Upadhyay & W.B. Kendr., Mycologia 67: 800. 1975 ≡ *Ceratocystis minuta-bicolor* R.W. Davidson, Mycopath. Mycol. Appl. 28: 280. 1966 ≡ *Hyalorhinocladiella minuta-bicolor* H.P. Upadhyay & W.B. Kendr., Mycologia 67: 800. 1975 ≡ *Ophiostoma minuta-bicolor* (R.W. Davidson) Hausner, J. Reid & Klassen, Mycol. Res. 97: 631. 1993 = *Ceratocystis pallida* H.D. Griffin, Can. J. Bot. 46: 708. 1968.

Anamorph: hyalorhinocladiella-like (Upadhyay & Kendrick 1975).

Descriptions: Olchowecki & Reid (1974, p. 1688); Upadhyay (1981, p. 131, Figs 495–498); Benade *et al.* (1996, pp 892–895, Figs 1–10).

Phylogenetic data: Hausner *et al.* (1993a); Hausner & Reid (2003); Zipfel *et al.* (2006); Massoumi-Alamouti *et al.* (2007, 2009); Plattner *et al.* (2009); Hafez *et al*. (2012); De Beer & Wingfield (2012).

Note: The anamorph of *Cop. minuta-bicolor* is the type of *Hyalorhinocladiella*, treated under the Melbourne Code as a synonym of *Ceratocystiopsis* (De Beer & Wingfield 2012). The synonymy of *C. pallida* with *Cop. minuta-bicolor* was suggested by Upadhyay (1981). The name *C. pallida* should not be confused with *S. pallida* (Tubaki) Matsush. (Matsushima 1975).

Ceratocystiopsis neglecta (Kirschner & Oberw.) Z.W. de Beer & M.J. Wingf. ***comb. nov.*****, MB 801066** ≡ *Ophiostoma neglectum* Kirschner & Oberw., Can. J. Bot. 77: 247–252. 1999 (basionym).

Anamorph: hyalorhinocladiella-like.

Phylogenetic data: De Beer & Wingfield (2012).

Notes: DNA sequence data produced by De Beer & Wingfield (2012) for the ex-type isolate (CBS 100596) confirmed that this species belongs to *Ceratocystiopsis*. The sheathed ascospores, although shorter than typical for *Ceratocystiopsis*, and the hyalorhinocladiella-like anamorph with some penicillately branched conidiophores, are consistent with those of other species. The name should not be confused with *Ceratocystis neglecta* M. van Wyk, Jol. Roux & C. Rodas.

Ceratocystiopsis ochracea (H.D. Griffin) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 132. 1981 ≡ *Ceratocystis ochracea* H.D. Griffin, Can. J. Bot. 46: 706. 1968.

Anamorph: unknown.

Descriptions: Olchowecki & Reid (1974, p. 1688, Pl I, Fig. 21); Upadhyay (1981, p. 132, Figs 499–501).

Ceratocystiopsis pallidobrunnea (Olchow. & J. Reid) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 133. 1981 ≡ *Ceratocystis pallidobrunnea* Olchow. & J.

Reid, Can. J. Bot. 52: 1685. 1974 ≡ *Ophiostoma pallidobrunneum* (Olchow. & J. Reid) Hausner & J. Reid, Can. J. Bot. 81: 875. 2003.

Anamorph: hyalorhinocladiella-like (de Hoog 1993).

Description: Upadhyay (1981, p. 133, Figs 502–505).

Phylogenetic data: Hausner & Reid (2003); Plattner *et al.* (2009); Hafez *et al*. (2012); De Beer & Wingfield (2012).

Ceratocystiopsis parva (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 88. 2006 ≡ *Ceratocystis parva* Olchow. & J. Reid, Can. J. Bot. 52. 1686. 1974 ≡ *Ophiostoma parvum* (Olchow. & J. Reid) Hausner, J. Reid & Klassen, Mycol. Res. 97: 631. 1993.

Anamorph: hyalorhinocladiella-like, based on the protologue.

Phylogenetic data: Hausner *et al.* (1993a); Hafez *et al*. (2012); De Beer & Wingfield (2012).

Notes: Upadhyay treated this species as a synonym of *Cop. minima*, but Hausner *et al.* (1993c) showed that it is distinct from both *Cop. minima* and *Cop. minuta*. Plattner *et al.* (2009) were unable to amplify some markers for *Cop. parva.*

Ceratocystiopsis ranaculosa T.J. Perry & J.R. Bridges, *In* Bridges & Perry, Mycologia 79: 631. 1987 [as *'ranaculosus'*] ≡ *Ophiostoma ranaculosum* (T.J. Perry & J.R. Bridges) Hausner, J. Reid & Klassen, Mycol. Res. 97: 631. 1993.

Anamorph: sporothrix-like.

Description: Hsiau & Harrington (1997, p. 665).

Phylogenetic data: Hausner *et al.* (1993a, c, 2000); Gorton & Webber (2000); Hausner & Reid (2003); Gorton *et al.* (2004); Zipfel *et al.* (2006); Massoumi-Alamouti *et al.* (2007); Plattner *et al.* (2009); Hafez *et al*. (2012); De Beer & Wingfield (2012).

Ceratocystiopsis rollhanseniana (J. Reid, Eyjólfsd. & Hausner) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 88. 2006 ≡ *Ophiostoma rollhansenianum* J. Reid, Eyjólfsd. & Hausner, *In* Hausner *et al.*, Can. J. Bot. 81: 44. 2003.

Anamorph: hyalorhinocladiella-like.

Phylogenetic data: Hausner *et al.* (1993a) (as '*Ceratocystiopsis* sp. 2'); Zipfel *et al.* (2006); Plattner *et al.* (2009); Hafez *et al*. (2012); De Beer & Wingfield (2012).

Notes: The two ITS sequences produced for this species by Plattner *et al.* (2009) are identical and group near *G. galeiformis* (De Beer & Wingfield 2012), while the LSU, SSU and β-tubulin sequences group within *Ceratocystiopsis,* which is probably correct (Plattner *et al.* 2009, Hafez *et al.* 2012; De Beer & Wingfield 2012).

Ceratocystiopsis spinulosa (H.D. Griffin) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 136. 1981 ≡ *Ceratocystis spinulosa* H.D. Griffin, Can. J. Bot. 46: 713. 1968.

Anamorph: hyalorhinocladiella-like (de Hoog 1993). Anamorph first decribed by Olchowecki & Reid (1974).

Descriptions: Olchowecki & Reid (1974, pp 1687–1688, Pl. I Figs 12–15); Upadhyay (1981, p. 136, Figs 510–513).

Fragosphaeria Shear, Mycologia 15: 124. 1923 [type species *F. purpurea*]

Notes: For a discussion of this genus, see De Beer *et al.* (2012) and De Beer & Wingfield (2012).

Fragosphaeria purpurea Shear, Mycologia 15: 124. 1923 ≡ *Cephalotheca purpurea* (Shear) Chesters, Trans. Br. Mycol. Soc. 19(4): 262 1935.

Anamorph: sporothrix-like, based on description by Chesters (1935).

Description: Chesters (1935).

Phylogenetic data: Suh & Blackwell (1999); Kolařík & Hulcr (2009); Harrington *et al.* (2010); De Beer *et al*. (2012); De Beer & Wingfield (2012).

Fragosphaeria reniformis (Sacc. & Therry) Malloch & Cain, Can. J. Bot. 48: 1819. 1970 ≡ *Cephalotheca reniformis* Sacc. & Therry, *In* Saccardo, Michelia 2: 312. 1881.

Anamorph: sporothrix-like, based on description by Chesters (1935).

Description: Chesters (1935).

Phylogenetic data: Suh & Blackwell (1999); Kolařík & Hulcr (2009); Harrington *et al.* (2010); De Beer *et al*. (2012); De Beer & Wingfield (2012).

Graphilbum H.P. Upadhyay & W.B. Kendr., Mycologia 67: 800. 1975. emend. Z.W. de Beer, Seifert & M.J. Wingf [type species *Gra. sparsum*]
= *Ceratocystis* Ellis & Halst. section *Ips* H.P. Upadhyay *pro parte*, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 70. 1981.

Ascocarps dark brown to black, bases globose; necks dark brown to black, straight or slightly curved, cylindrical to tapered, less than 500 µm long; ostiole sometimes surrounded by ostiolar hyphae. Asci evanescent. Ascospores hyaline, aseptate, cylindrical to oblong, surrounded with a hyaline, gelatinous, ossiform to rectangular sheath. Synnematous anamorphs, when present, pesotum-like, stipes pale to darkly pigmented, conidiophores more or less biverticillate, conidiogenous cells extending percurrently, often with delayed conidial dehiscence giving the impression of sympodial extension, conidia aseptate. oblong or ellipsoidal, base truncate, in slimy masses. Mononematous anamorphs, when present, hyalorhinocladiella-like, with unbranched or sparingly branched conidiophores, conidiogenous cells and conidia similar to those of the synnematous anamorph. Phylogenetically classified in the *Ophiostomatales*. Associated with conifer-infesting bark beetles.

Note: De Beer & Wingfield (2012) showed that *Gra. sparsum* and the other species listed below formed a well-supported, distinct lineage within the *Ophiostomatales*. *Graphilbum* is thus re-introduced and redefined here to accommodate these taxa.

Upadhyay (1981) designated formal sections in *Ceratocystis*. Most species in his Section *Ips* are included in *Ophiostoma s.l.*, but four of the species are included here in *Graphilbum.*

Graphilbum brunneocrinitum (E.F. Wright & Cain) Z.W. de Beer & M.J. Wingf. ***comb. nov.,*** **MB 801068** ≡ *Ceratocystis brunneocrinita* E.F. Wright & Cain, Can. J. Bot. 39: 1218. 1961 (basionym).

Anamorph: hyalorhinocladiella-like.

Descriptions: Wright & Cain (1961, pp. 1218–1222, Figs 1–6, 21); Griffin (1968, p. 699); Olchowecki & Reid (1974, p. 1689, Figs 116–117); Upadhyay (1981, p. 75, Figs 242–246).

Notes: The morphology of the anamorph, ascospores and perithecia of *Gra. tubicolle* closely resemble those of *Gra. nigrum* and other *Graphilbum* spp. Although no DNA sequences are available for this species, it clearly does not belong in *Ceratocystis* but in *Graphilbum*.

Graphilbum curvicolle (Olchow. & J. Reid) Z.W. de Beer & M.J. Wingf. , ***comb. nov.,*** **MB 801069** ≡ *Ceratocystis curvicollis* Olchow. & J. Reid, Can. J. Bot. 52: 1690. 1974 (basionym).

Anamorph: hyalorhinocladiella-like*.*

Description: Olchowecki & Reid (1974, pp 1690–1691, Figs 121–131).

Phylogenetic data: Hausner & Reid (2003); De Beer & Wingfield (2012).

Notes: Treated by Upadhyay (1981) as synonym of *O. nigrum*, LSU sequences differ by 5 bp (Hausner & Reid 2003). De Beer & Wingfield (2012) showed that this species groups in *Graphilbum*.

Graphilbum fragrans (Math.-Käärik) Z.W. de Beer, Seifert & M.J. Wingf. , ***comb. nov.,*** **MB 801070** ≡ *Graphium fragrans* Math.-Käärik, Medd. Skogsforskninginst. 43: 59. 1954 (basionym) ≡ *Pesotum fragrans* (Math.-Käärik) Okada & Seifert, Can. J. Bot. 76: 1503. 1998.

Anamorph: pesotum-like.

Descriptions: Harrington *et al.* (2001, p. 127, Figs 37–40); Jacobs *et al.* (2003c, pp 325–326, Figs 22–25); Jacobs & Seifert (2003, pp 79–80, Figs 1–5); Paciura *et al.* (2010b, p. 84, Figs 7, 11, 18).

Phylogenetic data: Okada *et al.* (1998), Harrington *et al*. (2001), Jacobs *et al*. (2003c); Kim *et al.* (2003); Thwaites *et al*. (2005); Zhou *et al*. (2006); Kim *et al.* (2007); Romón *et al.* (2007); Kamgan Nkuekam *et al*. (2008a); Lu *et al.* (2009a); Jankowiak & Kolařík (2010); Paciura *et al.* (2010b); Hafez *et al.* (2012).

Notes: This species seems to consist of several species (De Beer & Wingfield 2012). Harrington *et al.* (2001) showed that an isolate (CBS 219.83) considered authentic for *P. fragrans* by Okada *et al*. (1998), and recently also Hafez *et al.* (2012), actually represented another species. They suggested that CBS 279.54 should instead be treated as authentic for the type of *P. fragrans* (Harrington *et al.* 2001).

Graphilbum microcarpum (Yamaoka & Masuya) Z.W. de Beer & M.J. Wingf., ***comb. nov.,*** **MB 801071** ≡ *Ophiostoma microcarpum* Yamaoka & Masuya, *In* Yamaoka *et al.*, Mycoscience 45: 280. 2004 (basionym).

Anamorph: pesotum-like.

Phylogenetic data: De Beer & Wingfield (2012); Masuya *et al.* (2012).

Notes: An ITS sequence produced by Masuya *et al.* (2012) groups clearly within *Graphilbum* (De Beer & Wingfield 2012). The name should not be confused with *Ceratostomella microcarpa* (= *Ceratocystis microcarpa)* (see Section C.1).

Graphilbum nigrum (R.W. Davidson), Z.W. de Beer & M.J. Wingf. , ***comb. nov.,*** **MB 801072** ≡ *Ceratocystis nigra* R.W. Davidson, Mycologia 50: 662. 1958 (basionym) ≡ *Ophiostoma nigrum* (R.W. Davidson) de Hoog & Scheffer, Mycologia 76: 297. 1984.

Anamorph: hyalorhinocladiella-like.

Descriptions: Griffin (1968, pp 705–706), Olchowecki & Reid (1974, p. 1695), Upadhyay (1981, p. 81, Figs 277–285).

Phylogenetic data: Hausner *et al.* (1993b); Hausner & Reid (2003).

Notes: An LSU sequence places this species *Graphilbum* (De Beer & Wingfield 2012).

Graphilbum rectangulosporium (R.W. Davidson), Z.W. de Beer & M.J. Wingf., ***comb. nov.,*** **MB 801073** ≡ *Ophiostoma rectangulosporium* Ohtaka, Masuya & Yamaoka, *In* Ohtaka *et al.*, Can. J. Bot. 84: 290. 2006 (basionym).

Anamorph: not observed.

Description: Ohtaka *et al.* (2006, pp 290–292, Fig. 5).

Phylogenetic data: Ohtaka *et al.* (2006); Lu *et al.* (2009a); Paciura *et al.* (2010b); De Beer & Wingfield (2012).

Notes: This species groups within *Graphilbum* based on LSU and ITS sequences (De Beer & Wingfield 2012).

Graphilbum sparsum H.P. Upadhyay & W.B. Kendr., Mycologia 67: 800. 1975 ≡ *Ceratocystis sparsa* R.W. Davidson, Mycologia 63: 14. 1971 ≡ *Ophiostoma sparsum* (R.W. Davidson) de Hoog & Scheffer, Mycologia 76: 297. 1984 ≡ *Pesotum sparsum* (H.P. Upadhyay & W.B. Kendr.) G. Okada & Seifert, *In* Okada *et al.*, Can. J. Bot. 76: 1504. 1998.

Anamorph: pesotum-like.

Descriptions: Upadhyay (1981, p. 83, Figs 290–294); Seifert & Okada (1993, p. 32, Fig. 3A).

Phylogenetic data: Hausner & Reid (2003).

Notes: *Graphilbum sparsum* is the type species of the genus (Upadhyay & Kendrick 1975), re-introduced here to accommodate species previously treated in the *P. fragrans* complex (De Beer & Wingfield 2012).

Graphilbum tubicolle (Olchow. & J. Reid) Z.W. de Beer & M.J. Wingf. ***comb. nov.*, MB 801074** ≡ *Ceratocystis tubicollis* Olchow. & J. Reid, Can. J. Bot. 52: 1694. 1974 (basionym).

Anamorph: hyalorhinocladiella-like (Upadhyay 1981).

Descriptions: Olchowecki & Reid (1974, pp 1694–1695, Figs 172–182); Upadhyay (1981, p. 84).

Notes: The morphology of the anamorph, ascospores and perithecia of *Gra. tubicolle* closely resemble those of *Gra. nigrum* and other *Graphilbum* spp. Although no DNA sequences are available for this species, it clearly does not be classified in *Ceratocystis* but in *Graphilbum*.

Leptographium Lagerb. & Melin, *In* Lagerberg *et al.*, *Svenska SkogsvFör. Tidskr.* 25: 257. 1927 [type species *L. lundbergii*]
= *Scopularia* Preuss, Linnaea 24: 133. 1851 [*nom. illegit.*, Art. 52.1] [type species *Sc. venusta*, see *L. lundbergii*]
?= Grosmannia Goid., Boll. Staz. Patol. Veg. Roma 16: 31. 1936. emend. Z.W. de Beer, Zipfel & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 89. 2006. Teleomorphic synonym. [type species *G. penicillata*]
?= *Verticicladiella* S. Hughes, Can. J. Bot. 31: 653. 1953. Anamorphic synonym. [type species *L. abietinum*]
?= *Europhium* A.K. Parker, Can. J. Bot. 35: 175. 1957. Teleomorphic synonym. [type species *O. trinacriforme*]
?= Phialographium H.P. Upadhyay & W.B. Kendr., Mycologia 66: 183. 1974. Anamorphic synonym. [type species *G. sagmatospora*]
= *Ceratocystis* Ellis & Halst. section *Ceratocystis pro parte*, *In* Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 32. 1981.
?= *Graphiocladiella* H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis*, p. 138. 1981. Anamorphic synonym. [type species *G. clavigera*]
?= *Esteya* J.Y. Liou, J.Y. Shih & Tzean, Mycol. Res. 103: 243. 1999. Anamorphic synonym. [type species *E. vermicola*]
?= *Dryadomyces* Gebhardt, Mycol. Res. 109: 693. 2005. Anamorphic synonym. [type species *D. amasae*]

Notes: De Beer & Wingfield (2012) showed that *Leptographium s.l.* is not a well supported monophyletic clade. The type species of *Grosmannia* forms a strong monophyletic lineage designated as the *G. penicillioides* complex in *Leptographium s.l.*, the generic status of this lineage needs reconsideration. For the interim, *Grosmannia* is listed as possible synonym for *Leptographium*.

Wingfield (1985), Harrington (1988) and Jacobs & Wingfield (2001) treated *Verticicladiella* as synonym of *Leptographium*. The type species, *L. abietinum*, groups in the *G. penicillata* complex (De Beer & Wingfield 2012).

The synonymy of *Europhium* with *Grosmannia* as suggested by Zipfel *et al.* (2006) was questioned by De Beer & Wingfield (2012) because the generic placement of *O. trinacriforme* remains uncertain.

Upadhyay & Kendrick (1974, 1975) and Upadhyay (1981) separated the synnematous anamorphs of the *Ophiostomatales* in several distinct genera based on morphological differences, but Okada *et al*. (1998) treated all these genera as synonyms of *Pesotum*. *Pesotum* is now a synonym of *Ophiostoma s.str.* (see under *Ophiostoma* above), and the type species of two of these genera, *Phialographium* and *Graphiocladiella*, group in *Leptographium s.l.* (De Beer & Wingfield 2012). Because the delineation of genera within *Leptographium s.l.* needs further study, the current status of these two genera is presently uncertain.

Upadhyay (1981) designated official sections in *Ceratocystis*. Most species in his Section *Ceratocystis* are here included in *Leptographium s.l.*

The type species of the monotypic nematophagous genus, *Esteya*, groups peripherally to the *R. sulphurea* complex in *Leptographium s.l.* This complex also contains the type species of the ambrosial genus, *Dryadomyces*, and three *Raffaelea* spp. The generic status of both *Dryadomyces* and *Esteya* needs to be reassessed (De Beer & Wingfield 2012).

Grosmannia abieticola (Yamaoka & Masuya) Masuya & Yamaoka, *In* Seifert & Wingfield eds., Ophiostomatoid fungi: expanding frontiers, p. ***. 2012 ≡ *Ophiostoma abieticola* Yamaoka & Masuya, *In* Yamaoka *et al.*, Mycoscience 45: 281. 2004.

Anamorph: pesotum-like.

Description: Masuya *et al.* (2012).

Notes: This species groups peripherally to the *G. penicillata* complex based on rDNA sequences (De Beer & Wingfield 2012; Masuya *et al.* 2012). The name should not be confused with *L. abieticolens*.

Leptographium abieticolens K. Jacobs & M.J. Wingf., Mycoscience 41: 599. 2000.

Description: Jacobs & Wingfield (2001, pp 46–48, Figs 19–21).

Phylogenetic data: Jacobs *et al.* (2001d); Kim *et al.* (2004, 2005c); Masuya *et al.* (2004); Massoumi Alamouti *et al.* (2006); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Leptographium abieticolens* is part of the *G. penicillata* complex (Six *et al.* 2011; De Beer & Wingfield 2012). The name should not be confused with *G. abieticola*.

Leptographium abietinum (Peck) M.J. Wingf., Trans. Br. Mycol. Soc. 85: 92. 1985 ≡ *Sporocybe abietina* Peck, N. Y. State Museum Rep. 31: 45. 1879 ≡ *Periconia abietina* (Peck) Sacc., Syll. Fung. 4: 273. 1886 ≡ *Verticicladiella abietina* (Peck) S. Hughes, Can. J. Bot. 31: 653. 1953 = *Leptographium engelmannii* R.W. Davidson, Mycologia 47: 59. 1955.

Descriptions: Kendrick (1962, pp 773–776, Fig. 1, 9A–C); Jacobs *et al.* (1998, p. 1662, Figs 2, 4, 6); Jacobs & Wingfield (2001, pp 48–51, Figs 22–24).

Phylogenetic data: Jacobs *et al.* (2001d, 2005, 2006, 2010); Kim *et al.* (2004, 2005c, d); Masuya *et al*. (2004); Massoumi Alamouti *et al.* (2006, 2009); Zhou *et al*. (2008); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Leptographium abietinum is* part of the *G. penicillata* complex (Six *et al.* 2011; Linnakoski *et al.* 2012; De Beer & Wingfield 2012). Jacobs *et al.* (1998) and Jacobs & Wingfield (2001) suggested that *L. engelmannii* is a synonym of *L. abietinum*. This species name should not be confused with *O. abietinum*.

Grosmannia abiocarpa (R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 89. 2006 ≡ *Ceratocystis abiocarpa* R.W. Davidson, Mycopath. Mycol. Appl. 28: 273. 1966 ≡ *Ophiostoma abiocarpum* (R.W. Davidson) T.C. Harr., Mycotaxon 28: 41. 1987.

Anamorph: leptographium-like (Upadhyay 1981).

Descriptions: Olchowecki & Reid (1974, p. 1709); Upadhyay (1981, p. 87, Figs 295–302).

Phylogenetic data: Jacobs *et al.* (2001d)*;* Masuya *et al*. (2004); Greif *et al.* (2006); Massoumi Alamouti *et al.* (2006, 2007, 2009); Harrington *et al.* (2010); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al.* (2012); De Beer & Wingfield (2012).

Notes: *Grosmannia abiocarpa* is part of the *G. penicillata* complex (Six *et al.* 2011; Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Grosmannia aenigmatica (K. Jacobs, M.J. Wingf. & Yamaoka) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 89. 2006 ≡ *Ophiostoma aenigmaticum* K. Jacobs, M.J. Wingf. & Yamaoka, *In* Jacobs *et al.*, Mycol. Res. 102: 291. 1998 ≡ *Leptographium* *aenigmaticum* K. Jacobs, M.J. Wingf. & Yamaoka, *In* Jacobs *et al.*, Mycol. Res. 102: 291. 1998.

Anamorph: leptographium-like.

Description: Jacobs & Wingfield (2001, pp 52–55, Figs 25–27).

Phylogenetic data: Jacobs *et al.* (2004, 2005, 2006, 2010); Masuya *et al.* (2005); Massoumi Alamouti *et al.* (2006, 2010); Zipfel *et al.* (2006); Zhou *et al*. (2008); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); Jacobs *et al.* (2012); De Beer & Wingfield (2012).

Notes: This species is part of the *G. piceiperda* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Grosmannia alacris T.A. Duong, Z.W. de Beer & M.J. Wingf., *In* Duong *et al.*, Mycologia 104: 723. 2012 = *Verticicladiella alacris* M.J. Wingf. & Marasas, Trans. Br. Mycol. Soc. 75: 22. 1980 ≡ *Leptographium alacre* (M.J. Wingf. & Marasas) M. Morelet, Ann. Soc. Sci. Nat. Arch. Toulon et du Var 40: 44. 1988 [*nom. inval.*, Art. 33.4]

Anamorph: leptographium-like.

Descriptions: Wingfield & Marasas (1980b, pp 22–25, Figs 1–26); Duong *et al.* (2012, pp 723–724, Fig. 6).

Phylogenetic data: Duong *et al*. (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Wingfield & Marasas (1981) suggested the synonymy of *L. alacre* with *L. serpens*, which was accepted in subsequent studies (Harrington 1988, Jacobs & Wingfield 2001). Duong *et al.* (2012) showed that the two species were distinct based on a five gene phylogeny, and they discovered and described the teleomorph of the species. Their data confirmed that to date the true *G. serpens* has only been found in Italy, and that most other reports of *G. serpens* actually represent *G. alacris*, implying that *G. alacris* has the widest distribution in the *G. serpens* complex.

Leptographium albopini M.J. Wingf., T.C. Harr. & Crous, Can. J. Bot. 72: 234. 1994.

Descriptions: Wingfield *et al.* (1994b, pp 234–237, Figs 27–39); Jacobs & Wingfield (2001, pp. 55–57, Figs 28–30).

Phylogenetic data: Jacobs *et al.* (2001d); Masuya *et al.* (2004); Massoumi Alamouti *et al.* (2006); Paciura *et al*. (2010a); Six *et al.* (2011); Duong *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Leptographium albopini* forms a distinct lineage close to, but distinct from. the *L. lundbergii* and *G. clavigera* species complexes in *Leptographium s.l.* (Six *et al.* 2011; Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Leptographium alethinum K. Jacobs, M.J. Wingf. & Uzunovic, Mycol. Res. 105: 493. 2001.

Descriptions: Jacobs *et al.* (2001, pp 492–495, Figs 1–7); Jacobs & Wingfield (2001, pp 57–59, Figs 31–33).

Phylogenetic data: Jacobs *et al.* (2001d, 2004); Kim *et al.* (2004, 2005d); Masuya *et al*. (2004); Massoumi Alamouti *et al.* (2006); Lu *et al.* (2009b); Paciura *et al.* (2010a); Six *et al.* (2011); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Leptographium alethinum* forms a distinct lineage close to, but distinct from, the *L. lundbergii* and *G. clavigera* species complexes in *Leptographium s.l.* (Six *et al.* 2011; De Beer & Wingfield 2012).

Leptographium altius Paciura, Z.W. de Beer & M.J. Wingf., *In* Paciura *et al.*, Persoonia 25: 106. 2010.

Description: Paciura *et al*. (2010a, p. 106, Fig. 7h-m).

Phylogenetic data: Paciura *et al*. (2010a); Duong *et al.* (2012); Linnakoski *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *G. penicillata* complex (Paciura *et al*. 2010a; Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Raffaelea amasae (Gebhardt) T.C. Harr., Mycotaxon 111: 350. 2010 ≡ *Dryadomyces amasae* Gebhardt, Mycol. Res. 109: 693. 2005.

Description: Gebhardt *et al*. (2005, pp 690–694, Figs 5–7).

Phylogenetic data: Gebhardt *et al.* (2005); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Raffaelea amasae* is the type species of *Dryadomyces* (Gebhardt *et al*. 2005). It is part of the *R. sulphurea* complex in *Leptographium s.l.* and does not belong in *Raffaelea s.str.* (De Beer & Wingfield 2012)

Grosmannia americana (K. Jacobs & M.J. Wingf.) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 89. 2006 ≡ *Ophiostoma americanum* K. Jacobs & M.J. Wingf., *In* Jacobs *et al.*, Can. J. Bot. 75: 1318. 1997 ≡ *Leptographium americanum* K. Jacobs & M.J. Wingf., Can. J. Bot. 75: 1318. 1997.

Anamorph: leptographium-like.

Descriptions: Jacobs *et al.* (1997b, pp 1317–1320, Figs 1–11); Jacobs & Wingfield (2001, pp 60–63, Figs 34–36).

Phylogenetic data: Jacobs *et al*. (2001a, d, 2005, 2006, 2010); Kim *et al.* (2004, 2005d); Masuya *et al*. (2004); Greif *et al.* (2006); Massoumi Alamouti *et al.* (2006); Zhou *et al*. (2008); Lu *et al.* (2009a); Mullineux & Hausner (2009); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al.* (2012); De Beer & Wingfield (2012); Jacobs *et al.* (2012).

Notes: *Grosmannia americana* is part of the *G. penicillata* complex (Six *et al.* 2011; Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Grosmannia aoshimae (Ohtaka, Masuya & Yamaoka) Masuya & Yamaoka, *In* Seifert & Wingfield eds., Ophiostomatoid fungi: expanding frontiers, p. ***. 2012 ≡ *Ophiostoma aoshimae* Ohtaka, Masuya & Yamaoka, *In* Ohtaka *et al.*, Can. J. Bot. 84: 289. 2006 = *Ceratocystis polygrapha* Aoshima, Ph.D. thesis, University of Tokyo: 12. 1965 [*nom. inval*., Art. 29.1, 36.1]

Anamorph: unknown.

Descriptions: Aoshima (1965, p. 12, Figs 40–41); Masuya *et al*. (2012).

Phylogenetic data: Ohtaka *et al.* (2006); De Beer & Wingfield (2012); Masuya *et al.* (2012).

Notes: This species is part of *G. penicillioides* complex based on ITS sequence (De Beer & Wingfield 2012).Ohtaka *et al.* (2006) suggested that the description of the invalid species *C. polygrapha* corresponds with that of *G. aoshimae*.

Grosmannia aurea (R.C. Rob. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 89. 2006 ≡ *Europhium aureum* R.C. Rob. & R.W. Davidson, *In* Robinson-Jeffrey & Davidson, Can. J. Bot. 46: 1525. 1968 ≡ *Ceratocystis aurea* (R.C. Rob. & R.W. Davidson) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 37. 1981 ≡ *Leptographium aureum* M.J. Wingf., Trans. Br. Mycol. Soc. 85: 92. 1985 ≡ *Ophiostoma aureum* (R.C. Rob. & R.W. Davidson) T.C. Harr., Mycotaxon 28: 41. 1987.

Anamorph: leptographium-like.

Descriptions: Robinson-Jeffrey & Davidson (1968, p. 1525, Figs 7–9, 12c); Upadhyay (1981, p. 37, Figs 31–36); Jacobs & Wingfield (2001, pp 66–70, Figs 40–42); Lee *et al.* (2003, pp 1107–1109, Figs 1–15).

Phylogenetic data: Hausner *et al.* (1992b, 2000, 2005); Jacobs *et al.* (2001d, 2004, 2005, 2006, 2010); Lee *et al.* (2003, 2005); Lim *et al.* (2004); Kim *et al.* (2005d); Masuya *et al.* (2004, 2005); Massoumi Alamouti *et al.* (2006); Zipfel *et al.* (2006); Zhou *et al*. (2008); Lu *et al.* (2009a, b); Mullineux & Hausner (2009); Matsuda *et al.* (2010); Paciura *et al.* (2010a); Roe *et al.* (2010); Six *et al*. (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012); Jacobs *et al.* (2012).

Notes: Hausner *et al.* (2005) suggested that *L. wingfieldii* and *L. terebrantis* are possible synonyms of *L. aureum*. However, Roe *et al*. (2010) and Six *et al*. (2011) showed that these species are distinct members of the *G. clavigera* complex.

Leptographium bhutanense X.D. Zhou, K. Jacobs & M.J. Wingf., *In* Zhou *et al.*, Persoonia 21: 6. 2008.

Description: Zhou *et al.* (2008, pp 6–7, Figs 3–4).

Phylogenetic data: Zhou *et al*. (2008); Paciura *et al*. (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *L. procerum* complex (Six *et al.* 2011; Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Leptographium bistatum J.J. Kim & G.H. Kim, *In* Kim *et al*., Mycol. Res. 108: 701. 2004.

Description: Kim *et al.* (2004, pp 701–72, Figs 1–13).

Phylogenetic data: Kim *et al.* (2004); Massoumi Alamouti *et al.* (2006); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Leptographium bistatum* is part of the *G. penicillata* complex (Six *et al.* 2011; Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Grosmannia cainii (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 89. 2006 ≡ *Ceratocystis cainii* Olchow. & J. Reid, Can. J. Bot. 52: 1697. 1974 ≡ *Ophiostoma cainii* (Olchow. & J. Reid) T.C. Harr., Mycotaxon 28: 41. 1987.

Anamorph: pesotum-like.

Descriptions: Upadhyay (1981, p. 39, Figs 43–47); Seifert & Okada (1993, p. 32, Fig. 3D).

Phylogenetic data: Hausner *et al.* (2000); Masuya *et al*. (2004); Kim *et al.* (2005d); Six *et al*. (2011); Duong *et al.* (2012); De Beer & Wingfield (2012).

Notes: *Grosmannia cainii* forms a lineage of its own, distinct from other species complexes in *Leptographium s.l.* (De Beer & Wingfield 2012).

Leptographium calophylli (Wiehe) J.F. Webber, K. Jacobs & M.J. Wingf., Mycol. Res. 103: 1589. 1999 ≡ *Haplographium calophylli* Wiehe, Mycol. Pap. 29: 5. 1949 ≡ *Verticillium calophylli* (Wiehe) W. Gams, *In Cephalosporium-artige Schimmelpilze*: 206. 1971.

Descriptions: Wiehe (1949, pp 3–5, Figs 2–50); Webber *et al.* (1999, pp 1589–1592, Figs 1–12); Jacobs & Wingfield (2001, pp 76–78, Figs 49–51).

Notes: Teleomorph unknown. The morphology of *L. calophylli* differs from that of all other *Leptographium* spp. In the absence of DNA sequences, it is not possible to assign this species to a complex.

Leptographium castellanum T.A. Duong, Z.W. de Beer & M.J. Wingf., *In* Duong *et al.*, Mycologia 104: 726. 2012.

Description: Duong *et al.* (2012, pp 726–727, Fig. 9).

Phylogenetic data: Duong *et al*. (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *G. serpens* complex (Duong *et al*. 2012; De Beer & Wingfield 2012).

Leptographium celere Paciura, Z.W. de Beer & M.J. Wingf., *In* Paciura *et al.*, Persoonia 25: 100. 2010.

Description: Paciura *et al.* (2010a, pp100–102, Fig. 4g-l).

Phylogenetic data: Paciura *et al*. (2010a); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. In common with *L. manifestum*, *L. celere* groups in the *L. procerum* complex based on rDNA, but in the *L. lundbergii* complex based on β-tubulin and EF-1α sequences (Paciura *et al*. 2010a; Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Leptographium chlamydatum K. Jacobs, M.J. Wingf. & H. Solheim, *In* Jacobs *et al*., Mycol. Progress 9: 73. 2010.

Description: Jacobs *et al.* (2010, pp 73–74, Figs 2–3).

Phylogenetic data: Jacobs *et al.* (2010); Duong *et al.* (2012); Linnakoski *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *G. penicillata* complex (Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Grosmannia clavigera (R.C. Rob. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 90. 2006 ≡ *Europhium clavigerum* R.C. Rob. & R.W. Davidson, *In* Robinson-Jeffrey & Davidson, Can. J. Bot. 46: 1523. 1968 ≡ *Ceratocystis clavigera* (R.C. Rob. & R.W. Davidson) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 40. 1981 ≡ *Graphiocladiella clavigera* H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 40. 1981 ≡ *Ophiostoma clavigerum* (R.C. Rob. & R.W. Davidson) T.C. Harr., Mycotaxon 28: 41. 1987 ≡ *Pesotum clavigerum* (H.P. Upadhyay) G. Okada & Seifert, *In* Okada *et al.*, Can. J. Bot. 76: 1503. 1998 ≡ *Leptographium clavigerum* (H.P. Upadhyay) T.C. Harr., Six & McNew, *In* Six *et al.*, Mycologia 95: 791. 2003.

Anamorph: pesotum-like.

Descriptions: Robinson-Jeffrey & Davidson (1968, pp 1523–1525, Figs 1–6, 12a); Upadhyay (1981, p. 38, Figs 48–57); Tsuneda & Hiratsuka (1984, pp 2619–2623, Figs 1–24); Lee *et al*. (2003, pp 1108–1109); Six *et al.* (2003, pp 782–783, 786–787).

Phylogenetic data: Hausner *et al.* (1992b); Six *et al.* (2003); Lee *et al.* (2003, 2005); Kim *et al.* (2004, 2005d); Lim *et al.* (2004, 2005); Greif *et al*. (2006); Masuya *et al.* (2005); Massoumi Alamouti (2006, 2009, 2011); Lu *et al.* (2009a, b); Paciura *et al.* (2010a); Roe *et al.* (2010, 2011); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Note: The anamorph of *G. clavigera* is the type species of *Graphiocladiella* (Upadhyay 1981). Lee *et al.* (2007) and Massoumi Alamouti *et al.* (2011) showed that the *G. clavigera* population in British Columbia, Canada consists of two distinct groups, representing sibling species. One species remains to be described as new. The complete genome of *G. clavigera* has been sequenced, making it the first ophiostomatoid genome published (Diguistini *et al*. 2009, 2011). Roe *et al.* (2010, 2011) conducted a population and phylogeographic study based on five gene regions on *G. clavigera*, showing that recombination in this species is rare, which suggests that it reproduce sexually infrequently in nature.

Leptographium conjunctum Paciura, Z.W. de Beer & M.J. Wingf., *In* Paciura *et al.*, Persoonia 25: 99. 2010.

Description: Paciura *et al.* (2010a, pp 99–100, Fig. 4a-f).

Phylogenetic data: Paciura *et al.* (2010a); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012)

Notes: Teleomorph unknown. This species ispart of the *L. lundbergii* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Grosmannia crassivaginata (H.D. Griffin) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 90. 2006 ≡ *Ceratocystis crassivaginata* H.D. Griffin, Can. J. Bot. 46: 701. 1968 ≡ *Ceratocystiopsis crassivaginata* (H.D. Griffin) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 123. 1981 ≡ *Leptographium crassivaginatum* M.J. Wingf., Trans. Br. Mycol. Soc. 85: 92. 1985 ≡ *Ophiostoma crassivaginatum* (H.D. Griffin) T.C. Harr., Mycotaxon 28: 41. 1987.

Anamorph: leptographium-like.

Descriptions: Olchowecki and Reid (1974, p. 1679, Pl. I Fig. 16); Upadhyay (1981, p. 123, Figs 440–444); Jacobs & Wingfield (2001, pp 81–84, Figs 55–57).

Phylogenetic data: Hausner *et al.* (1993c, 2000); Jacobs *et al.* (2001d); Hausner & Reid (2003); Masuya *et al.* (2004); Kim *et al.* (2005d); Massoumi Alamouti *et al.* (2006); Zipfel *et al.* (2006); Paciura *et al.* (2010a); Mullineux *et al*. (2011); Six *et al.* (2011); Duong *et al*. (2012); De Beer & Wingfield (2012).

Notes: This species groups in a lineage with *L. piriforme*, distinct from other species complexes in *Leptographium s.l.* (De Beer & Wingfield 2012).

Grosmannia cucullata (H. Solheim) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 90. 2006 ≡ *Ophiostoma cucullatum* H. Solheim, Nord. J. Bot. 6: 202. 1986 = *Graphium erubescens* Math.-Käärik, Medd. Skogsforskninginst. 43: 62. 1953 ≡ *Pesotum erubescens* (Math.-Käärik) G. Okada, Stud. Mycol. 45: 184. 2000 ≡ *Phialographium erubescens* (Math.-Käärik) T.C. Harr. & McNew, *In* Harrington *et al.*, Mycologia 93: 129. 2001.

Anamorph: pesotum-like.

Descriptions: Wingfield *et al.* (1989, pp 92–95, Figs 1–10), Yamaoka *et al.* (1997, pp 1220–1221). Of *Anamorph*: Harrington *et al.* (2001, pp 128–129, Figs 41–45).

Phylogenetic data: Hausner *et al.* (1992b, 1993b, 2000); Okada *et al.* (1998); Hausner *et al.* (2000); Harrington *et al.* (2001); Schroeder *et al.* (2001); Gebhardt *et al.* (2004, 2005); Greif *et al.* (2006); Massoumi Alamouti *et al.* (2009); Mullineux & Hausner (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); Paciura *et al.* (2010a); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Harrington *et al.* (2001) suggested that *P. erubescens* represented the anamorph of *G. cucullata* based on ITS sequences from the ex-type isolates of the two species, which differed by only two bp. However, the SSU sequences of the same two isolates from Hausner *et al*. (2000) and Okada *et al*. (2000) differ in 11 bp positions (see Fig. 2, De Beer *et al*. 2012). Furthermore, the SSU sequence of a Japanese isolate labelled as '*O. cucullatum*' by Okada *et al*. (1998), differ respectively in 5 and 19 bp from the ex-types of *G. cucullata* and *P. erubescens*. Linnakoski *et al*. (2012) did not include the ex-type of *P. erubescens* in their study, but showed that the species distinction of *G. cucullata* of *G. olivaceapini* in the *G. olivacea* complex is problematic. We thus suggest a reconsideration of the synonymy of *G. cucullata* and *P. erubescens*, and the status of the Japanese isolate and *G. olivaceapini*, using authentic isolates of all species and sequences from more gene regions.

Leptographium curviconidium Paciura, Z.W. de Beer & M.J. Wingf., *In* Paciura *et al.*, Persoonia 25: 104. 2010.

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

Phylogenetic data: Paciura *et al.* (2010a); Duong *et al.* (2012); Linnakoski *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *G. penicillata* complex (Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Leptographium curvisporum K. Jacobs, M.J. Wingf. & H. Solheim, *In* Jacobs *et al*., Mycol. Progress 9: 74. 2010.

Description: Jacobs *et al.* (2010, pp 74–75, Figs 4–5).

Phylogenetic data: Jacobs *et al.* (2010); Duong *et al.* (2012); Linnakoski *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Leptographium curvisporum* is part of the *G. penicillata* complex (Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Grosmannia davidsonii (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 90. 2006 ≡ *Ceratocystis davidsonii* Olchow. & J. Reid, Can. J. Bot. 52: 1698. 1974 ≡ *Ophiostoma davidsonii* (Olchow. & J. Reid) H. Solheim, Nord. J. Bot. 6: 203. 1986.

Anamorph: pesotum-like.

Descriptions: Upadhyay (1981, p. 42, Figs 58–62); Mouton *et al.* (1993, pp 376–377, Figs 15–18); Ohtaka *et al.* (2002, pp 154–156).

Phylogenetic data: Hausner *et al.* (2000); Masuya *et al*. (2004); Mullineux & Hausner (2009); Duong *et al.* (2012); Linnakoski *et al.* (2012); De Beer & Wingfield (2012).

Notes: This species is part of the *G. olivacea* species complex (Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Leptographium douglasii M.J. Wingf., T.C. Harr. & Crous, Can. J. Bot. 72: 231. 1994.

Descriptions: Wingfield *et al.* (1994b, pp 231–234, Figs 14–26); Jacobs & Wingfield (2001, pp 84–87, Figs 58–60).

Phylogenetic data: Jacobs *et al*. (2001d, 2004, 2005); Massoumi Alamouti *et al.* (2006); Zhou *et al*. (2008); Paciura *et al*. (2010a); Six *et al*. (2011); Duong *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species groups in the *G. wageneri* complex (Six *et al.* 2011); De Beer & Wingfield 2012). The name *L. douglasii* should not be confused with *C. douglasii* (see under *Ceratocystis*, section B.1).

Grosmannia dryocoetidis (W.B. Kendr. & Molnar) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 90. 2006 ≡ *Ceratocystis dryocoetidis* W.B. Kendr. & Molnar, Can. J. Bot. 43: 39. 1965 ≡ *Ophiostoma dryocoetidis* (W.B. Kendr. & Molnar) de Hoog & R.J. Scheff., Mycologia 76: 297. 1984 ≡ *Verticicladiella dryocoetidis* W.B. Kendr. & Molnar, Can. J. Bot. 43: 40. 1965 ≡ *Leptographium dryocoetidis* (W.B. Kendr. & Molnar) M.J. Wingf., Trans. Br. Mycol. Soc. 85: 92. 1985.

Anamorph: leptographium-like.

Descriptions: Kendrick & Molnar (1965, pp 39–43, Figs 1–3); Upadhyay (1981, p. 43, Figs 63–38); Jacobs & Wingfield (2001, pp 87–90, Figs 61–63).

Phylogenetic data: Hausner *et al.* (1993d, 2000); Jacobs *et al*. (2001a, d); Masuya *et al*. (2004); Kim *et al.* (2005d); Greif *et al.* (2006); Massoumi Alamouti *et al.* (2006); Mullineux & Hausner (2009); Harrington *et al.* (2010); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); De Beer & Wingfield (2012).

Notes: The ITS sequence (AF224333) of the ex-type strain of *G. dryocoetis* (CMW442), deposited by Jacobs *et al*. (2001a) is a chimeric sequence: the ITS 1 region is a 91% BLAST match of and aligns fairly well with a *G. laricis* sequence (GU134163), while the ITS 2 region is 98% similar to AJ538340, an unpublished sequence by Villarreal *et al*. of the ex-type isolate (CBS 376.66) of *G. dryocoetis*. The latter is thus the more reliable sequence and it places the species in the *G. penicillata* complex (Six *et al.* 2011; Duong *et al.* 2012; De Beer & Wingfield 2012).

Leptographium elegans M.J. Wingf., Crous & S.S. Tzean, Mycol. Res. 98: 783. 1994.

Descriptions: Wingfield *et al.* (1994a, pp 782–784, Figs 1–8); Jacobs & Wingfield (2001, pp 90–93, Figs 64–66).

Phylogenetic data: Jacobs *et al.* (2001d); Kim *et al.* (2004, 2005c); Masuya *et al*. (2004); Massoumi Alamouti *et al.* (2006); Six *et al*. (2011); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Leptographium elegans* forms a lineage between *Esteya vermicola* and the *R. sulphurea* complex in *Leptographium s.l.*, and is quite distinct from other *Leptographium* spp. (Six *et al*. 2011; De Beer & Wingfield 2012).

Leptographium eucalyptophilum K. Jacobs, M.J. Wingf. & Jol. Roux, S. Afr. J. Bot. 65: 390. 1999.

Descriptions: Jacobs *et al.* (1999, pp 389–390, Figs 1–7); Jacobs & Wingfield (2001, pp 93–96, Figs 67–69).

Phylogenetic data: Jacobs *et al.* (2001d); Masuya *et al.* (2004); Kim *et al.* (2005d); Massoumi Alamouti *et al.* (2006); Paciura *et al.* (2010a); Six *et al*. (2011); Duong *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *G. penicillata* complex (Six *et al*. 2011; De Beer & Wingfield 2012).

Leptographium euphyes K. Jacobs & M.J. Wingf., *In* Jacobs *et al.*, Mycol. Res. 105: 497. 2001.

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

Phylogenetic data: Jacobs *et al.* (2001d); Kim *et al.* (2004, 2005d); Masuya *et al*. (2004); Massoumi Alamouti *et al.* (2006); Paciura *et al.* (2010a); Six *et al*. (2011); Duong *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Leptographium euphyes* is part of the *G. penicillata* complex (Six *et al*. 2011; De Beer & Wingfield 2012).

Grosmannia europhioides (E.F. Wright & Cain) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 90. 2006 ≡ *Ceratocystis europhioides* E.F. Wright & Cain, Can. J. Bot. 39: 1222. 1961 ≡ *Ophiostoma europhioides* (E.F. Wright & Cain) H. Solheim, Nord. J. Bot. 6: 203. 1986 = *Ceratocystis shikotsuensis* Aoshima, Ph.D. thesis, University of Tokyo: 10. 1965 [*nom. inval*., Art. 29.1, 36.1]

Anamorph: leptographium-like (Solheim 1986).

Descriptions: Davidson *et al*. (1967, pp 929–930); Griffin (1968, pp 709, 713); Olchowecki & Reid (1974, p. 1699, Pl. XIII Figs 259–261); de Hoog & Scheffer (1984, p. 295, Fig. 2); Yamaoka *et al.* (1997, pp 1221–1222); Jacobs *et al.* (1998, pp. 290–291); Jacobs *et al.* (2000b, p. 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.* (2010a); Six *et al.* (2011); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Note: Upadhyay (1981) and Hutchison & Reid (1988a) treated *G. europhioides* as a synonym of *G. piceiperda*, but Solheim (1986), Harrington (1988), Yamaoka (1997) and Jacobs *et al.* (1998) considered it distinct*.* Harrington (1988) considered *G. pseudoeurophioides* a synonym of *G. europhioides*. Jacobs *et al.* (2000b) and Jacobs & Wingfield (2001) treated the latter two species as synonyms of *G. piceiperda*, but Hausner *et al.* (1993b, 2000) suggested that they are distinct from *G. europhioides*. Linnakoski *et al*. (2012) showed that isolates previously assigned to *G. piceiperda* represent at least five lineages. The status of these lineages should be reconsidered together with *G. europhioides* and *G. pseudoeurophioides*. Yamaoka *et al*. (1997) suggested that *C. shikotsuensis*, invalidly described by Aoshima (1965), was identical with *G. europhioides*. Masuya *et al.* (2012) suggested that the status of '*G. europhioides*' isolates from Japan needs reconsideration. All the lineages now represented by the name *G. europhioides* are part of the *G. piceiperda* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Grosmannia francke-grosmanniae (R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 90. 2006 ≡ *Ceratocystis francke-grosmanniae* R.W. Davidson, Mycologia 63: 6. 1971 ≡ *Ophiostoma francke-grosmanniae* (R.W. Davidson) de Hoog & R.J. Scheff., Mycologia 76: 297. 1984 ≡ *Leptographium francke-grosmanniae* .K. Jacobs & M.J. Wingf., Leptographium species, p. 99. 2001.

Anamorph: leptographium-like.

Descriptions: Upadhyay (1981, p. 45, Figs 73–78); Wingfield (1993, p. 48, Figs 6–7); Jacobs & Wingfield (2001, pp 99–102, Figs 73–75).

Phylogenetic data: Hausner *et al.* (2000); Jacobs *et al.* (2001d); Masuya *et al.* (2004); Kim *et al.* (2005d); Massoumi Alamouti *et al.* (2006); Zipfel *et al.* (2006); Mullineux & Hausner (2009); Matsuda *et al.* (2010); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); De Beer & Wingfield (2012) .

Notes: LSU sequences of *G. francke-grosmanniae* from the studies of Hausner *et al*. (2000) (ex-type ATCC22061), Jacobs *et al*. (2001a, d) (ex-type CMW445), and Zipfel *et al*.

(2006) (CMW2975), do not correspond. According to De Beer & Wingfield (2012), the sequence produced by Hausner *et al.* (2000) groups somewhere between the *L. lundbergii* and *G. olivacea* complexes, while that by Jacobs *et al.* (2001a, d) groups in the *G. penicillata* complex, and the one by Zipfel *et al.* (2006) close to *G. serpens* complex. An ITS sequence of ATCC22061 produced by Mullineux & Hausner (2009) also groups close in the *G. olivacea* complex (De Beer & Wingfield 2012). Although the treatment of the species in *Grosmannia* by Zipfel *et al.* (2006) is acceptable for the present, its exact placement within *Leptographium s.l.* needs to be determined.

Leptographium fruticetum Alamouti, J.J. Kim & C. Breuil, *In* Massoumi Alamouti *et al.*, Mycologia 98: 156. 2006.

Description: Massoumi Alamouti *et al.* (2006, pp 156–157, Figs 1–12).

Phylogenetic data: Massoumi Alamouti *et al.* (2006, 2009); Paciura *et al.* (2010a); Six *et al*. (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *G. penicillata* complex (Six *et al*. 2011; Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Grosmannia galeiformis (B.K. Bakshi) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 90. 2006 ≡ *Ceratocystis galeiformis* Bakshi, Mycol. Pap. 35: 13. 1951 ≡ *Ophiostoma galeiforme* (B.K. Bakshi) Math.-Käärik, Medd. Skogsforskninginst. 43: 47. 1953 [as '*galeiformis*']

Anamorph: leptographium- to pesotum-like*.*

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

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

Notes: An epitype was designated for *G. galeiformis* by Zhou *et al.* (2004b). Thwaites *et al.* (2005) treated *G. radiaticola* as synonym of *G. galeiformis* based on ITS sequences, but Kim *et al.* (2005d) showed with actin and β-tubulin sequences, and by mating behaviour, that the two species are distinct. Linnakoski *et al*. (2012) redefined the *G. galeiformis* complex and showed that two more lineages, probably representing undescribed species, exist within the complex. De Beer & Wingfield (2012) showed that *G. galeiformis* forms a well-supported lineage together with *G. radiaticola* within *Leptographium s.l.*

Leptographium gibbsii T.A. Duong, Z.W. de Beer & M.J. Wingf., *In* Duong *et al.*, Mycologia 104: 725. 2012.

Description: Duong *et al.* (2012, p. 725, Fig. 7).

Phylogenetic data: Duong *et al*. (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *G. serpens* complex (Duong *et al*. 2012; De Beer & Wingfield 2012).

Leptographium gracile Paciura, Z.W. de Beer & M.J. Wingf., *In* Paciura *et al.*, Persoonia 25: 103. 2010.

Description: Paciura *et al.* (2010a, pp 103–104, Figs 5h-m).

Phylogenetic data: Paciura *et al*. (2010a); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *L. procerum* complex (Paciura *et al.* 2010a; Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Grosmannia grandifoliae (R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 90. 2006 ≡ *Ceratocystis grandifoliae* R.W. Davidson, Mem. N.Y. Bot.

Gard. 28: 45. 1976 ≡ *Leptographium grandifoliae* M.J. Wingf., Trans. Br. Mycol. Soc. 85: 92. 1985 ≡ *Ophiostoma grandifoliae* (R.W. Davidson) T.C. Harr., Mycotaxon 28: 41. 1987.

Anamorph: leptographium-like.

Descriptions: Davidson (1976, pp 45–47, Figs 1–4); Upadhyay (1981, p. 46, Figs 79–84); Jacobs & Wingfield (2001, pp 102–106, Figs 76–78).

Phylogenetic data: Hausner *et al.* (2000); Jacobs *et al*. (2001d); Masuya *et al.* (2004); Massoumi Alamouti *et al.* (2006); Zipfel *et al.* (2006); Matsuda *et al.* (2010); Paciura *et al.* (2010a); Six *et al*. (2011); Duong *et al.* (2012); De Beer & Wingfield (2012).

Notes: This species forms a distinct lineage separate from other species complexes in *Leptographium s.l.* (Six *et al.* 2011; De Beer & Wingfield 2012). In some analyses, it groups with *L. pruni* (Massoumi Alamouti *et al.* (2006); Duong *et al*. 2012).

Leptographium guttulatum M.J. Wingf. & K. Jacobs, *In* Jacobs *et al.*, Mycologia 93: 382. 2001.

Descriptions: Jacobs *et al.* (2001a, pp 382–386, Figs 2–8); Jacobs & Wingfield (2001, p. 106–108. Figs 79–81).

Phylogenetic data: Jacobs *et al*. (2001a, d); Masuya *et al*. (2004); Greif *et al.* (2006); Paciura *et al.* (2010a); Six *et al*. (2011); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. The ITS and LSU sequences produced by Jacobs *et al*. (2001d) place *L. guttulatum* in either the *G. clavigera* or the *G. penicillata* complexes*.* A re-evalutation of its relationships is thus necessary (De Beer & Wingfield 2012).

Leptographium hughesii K. Jacobs, M.J. Wingf. & T.C. Harr., *In* Jacobs *et al.*, Can. J. Bot. 76: 1662. 1998.

Descriptions: Jacobs *et al.* (1998, pp 1662–1666, Figs 1, 3, 5, 7–13); Jacobs & Wingfield (2001, p.109–111, Figs 82–84).

Phylogenetic data: Jacobs *et al.* (2001d); Masuya *et al.* (2004); Kim *et al.* (2005d); Massoumi Alamouti *et al.* (2006); Paciura *et al.* (2010a); Six *et al*. (2011); Duong *et al.* (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Leptographium hughesii* is part of the *G. penicillata* complex (Six *et al*. 2011; De Beer & Wingfield 2012).

Grosmannia huntii (R.C. Rob.) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 91. 2006 ≡ *Ceratocystis huntii* R.C. Rob., *In* Robinson-Jeffrey & Grinchenko, Can. J. Bot. 42: 528. 1964 ≡ *Ophiostoma huntii* (R.C. Rob.) de Hoog & R.J. Scheff., Mycologia 76: 297. 1984 ≡ *Leptographium huntii* M.J. Wingf., Trans. Br. Mycol. Soc. 85: 92. 1985.

Anamorph: leptographium-like.

Descriptions: Robinson-Jeffrey & Grinchenko (1964, pp 528–531, Figs 1–17); Griffin (1968, p. 710, 713); Olchowecki & Reid (1974, p. 1699, Pl. XIII Figs 252, 256); Upadhyay (1981, p. 47, Figs 85–90); Wingfield (1993, p. 46, Fig. 3); Jacobs *et al.* (1998, pp 290–291); Jacobs & Wingfield (2001, pp 111–115, Figs 85–87).

Phylogenetic data: Jacobs *et al*. (2001d, 2004, 2006); Lim *et al.* (2004); Masuya *et al.* (2004, 2005); Kim *et al.* (2005a, c, d); Lee *et al.* (2005); Thwaites *et al.* (2005); Massoumi Alamouti *et al.* (2006); Zipfel *et al.* (2006); Zhou *et al*. (2008); Mullineux & Hausner (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); Paciura *et al.* (2010a); Kim *et al.* (2011); Six *et al*. (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012); Jacobs *et al.* (2012).

Notes: *Grosmannia huntii* groups peripherally to the *L. lundbergii* and *G. clavigera* complexes (Six *et al*. 2011; Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Grosmannia koreana (Masuya, J.J. Kim & M.J. Wingf.) Lu, Decock & Maraite, Antonie van Leeuwenhoek 96: 288. 2009 ≡ *Ophiostoma koreanum* Masuya, J.J. Kim & M.J. Wingf., *In* Masuya *et al.*, Mycotaxon 94: 168. 2005 = *Leptographium koreanum* J.J. Kim & G.H. Kim, Mycol. Res. 109: 278. 2005.

Anamorph: leptographium-like.

Phylogenetic data: Kim *et al.* (2005c); Masuya *et al.* (2005, 2012); Massoumi Alamouti *et al.* (2006); Lu *et al.* (2009b); Paciura *et al.* (2010a); Roe *et al.* (2010); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al.* (2012); De Beer & Wingfield (2012); Jacobs *et al.* (2012).

Notes: This species is part of the *L. lundbergii* complex (Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Grosmannia laricis (K. van der Westh., Yamaoka & M.J. Wingf.) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 91. 2006 ≡ *Ophiostoma laricis* K. van der Westh., Yamaoka & M.J. Wingf., Mycol. Res. 99: 1336. 1995 ≡ *Leptographium laricis* K. van der Westh., Yamaoka & M.J. Wingf., Mycol. Res. 99: 1336. 1995 = *Ceratocystis macrospora* Aoshima, Ph.D. thesis, University of Tokyo: 18. 1965 [*nom. inval*., Art. 29.1, 36.1]

Anamorph: leptographium-like.

Descriptions: Yamaoka *et al.* (1998, pp 371–372, Figs 16–20); Jacobs & Wingfield (2001, pp 115–118, Figs 88–90).

Phylogenetic data: Jacobs *et al*. (2001a, d, 2005, 2006, 2010); Masuya *et al.* (2004, 2005); Greif *et al*. (2006); Zipfel *et al.* (2006); Zhou *et al*. (2008); Mullineux & Hausner (2009); Harrington *et al.* (2010); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012); Jacobs *et al.* (2012).

Notes: Yamaoka *et al.* (1998) suggested that *C. macrospora* is the same fungus as *G. laricis*, which forms part of the *G. piceiperda* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012). This name should not be confused with *Graphium laricis,* which is a member of the *Microascales* (Jacobs *et al.* 2003b).

Leptographium latens Paciura, Z.W. de Beer & M.J. Wingf., *In* Paciura *et al.*, Persoonia 25: 104. 2010.

Description: Paciura *et al.* (2010a, p. 104, Figs 6a-f).

Phylogenetic data: Paciura *et al.* (2010a); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *L. procerum* complex (Paciura *et al.* 2010a; Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Grosmannia leptographioides (R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 91. 2006 ≡ *Ceratostomella leptographioides* R.W. Davidson, Mycologia 34: 657. 1942 ≡ *Ophiostoma leptographioides* (R.W. Davidson) Arx, Antonie van Leeuwenhoek 18: 211. 1952 ≡ *Ceratocystis leptographioides* (R.W. Davidson) J. Hunt, Lloydia 19: 28. 1956 ≡ *Leptographium leptographioides* .K. Jacobs & M.J. Wingf., Leptographium species, p. 118. 2001.

Anamorph: leptographium-like.

Descriptions: Hunt (1956, pp 28–29); Upadhyay (1981, p. 48, Figs 91–100); Jacobs & Wingfield (2001, pp 118–121, Figs 91–93).

Phylogenetic data: Jacobs *et al.* (2001d); Kim *et al.* (2005d); Zipfel *et al.* (2006); Matsuda *et al.* (2010); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); De Beer & Wingfield (2012).

Notes: This species forms a distinct lineage from other species complexes in *Leptographium s.l.* (Paciura *et al.* 2010a; Six *et al*. 2011; Duong *et al.* 2012; De Beer & Wingfield 2012).

Leptographium longiclavatum S.W. Lee, J.J. Kim & C. Breuil, Mycol. Res. 109: 1165. 2005.

Description: Lee *et al.* (2005, pp 1165–1167, Figs 1–13).

Phylogenetic data: Lee *et al*. (2005); Lu *et al.* (2009b); Massoumi Alamouti (2009, 2011); Paciura *et al.* (2010a); Roe *et al.* (2010, 2011); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *G.clavigera* complex (Six *et al*. 2011; De Beer & Wingfield 2012). The results of population study by Roe *et al.* (2010, 2011) suggest that this species does not reproduce sexually.

Leptographium lundbergii Lagerb. & Melin, *In* Lagerberg *et al*., Svenska SkogsvFör. Tidskr. 25: 257. 1927 [as *'Lundbergii'*] ≡ *Scopularia lundbergii* (Lagerb. & Melin) Goid., Boll. Staz. Patol. Veg. Roma 16: 39. 1936 [as *'Lundbergii'*]

?= *Scopularia venusta* Preuss, Linnaea 24: 133. 1851 [*nom. illegit*., Art. 53.1]

Descriptions: Lagerberg *et al*. (1927, pp 248–257, Figs 54–59); Barron (1972, pp 215–216, Fig. 129); Wingfield (1993, pp 46, 48, Figs 2, 8); Jacobs & Wingfield (2001, pp 121–123, Figs 94–96); Jacobs *et al*. (2005, pp 1153–1155, Figs 2–13).

Phylogenetic data: Jacobs *et al.* (2001d, 2004, 2005, 2006, 2010); Kim *et al.* (2004, 2005c, d); Masuya *et al.* (2004, 2005); Hausner *et al.* (2005); Lee *et al*. (2005); Greif *et al.* (2006); Massoumi Alamouti *et al.* (2006, 2009); Zhou *et al*. (2008); Lu *et al.* (2009a, b); Mullineux & Hausner (2009); Paciura *et al*. (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Note: *Leptographium lundbergii* is the type of *Leptographium* and the nominal species of the *L. lundbergii* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012). Jacobs *et al.* (2005) designated a neotype. No teleomorph has been observed for *L. lundbergii*. Kendrick (1964a) suggested that *Sc. venusta* was a possible synonym of *L. lundbergii*, but the condition of the type material was so poor that it was impossible to make a definite conclusion.

Leptographium manifestum Paciura, Z.W. de Beer & M.J. Wingf., *In* Paciura *et al.*, Persoonia 25: 102. 2010.

Description: Paciura *et al.* (2010a, p. 102, Figs 5a-g).

Phylogenetic data: Paciura *et al.* (2010a); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. In common with *L. celere*, *L. manifestum* groups in the *L. procerum* complex based on rDNA, but in the *L. lundbergii* complex based on β-tubulin and EF-1α sequences (Paciura *et al*. 2010a; Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Leptographium microsporum R.W. Davidson, J. Agr. Res. 50: 805. 1935 ≡ *Scopularia microspora* (R.W. Davidson) Goid., Boll. Staz. Patol. Veg. Roma 16: 39. 1936.

Description: Davidson (1935, pp 804–805, Figs 4A–C).

Note: Teleomorph unknown. Jacobs & Wingfield (2001) could not locate any authentic cultures or herbarium specimens for this species, but the name is validly published. Davidson (1935) considered *L. microsporum* similar to *L. penicillatum*, but this comparison should be interpreted with care considering that *L. penicillatum* and *L. lundbergii* were the only two known species at the time. Harrington (1988) suggested that Davidson's (1935) illustrations and the dimensions of the conidia resembled *L. procerum*. We thus treat the species as possibly distinct within *Leptographium*, but suggest neotypification using isolates from red gum and/or beech in the southern USA (Davidson 1935). The name *L. microsporum* should not be confused with *O. microsporum* or *Cs. microspora*.

Raffaelea montetyi M. Morelet, Ann. Soc. Sci. Nat. Arch. Toulon et du Var 50: 189. 1998.

Description: Morelet (1998, pp 189–191, Fig. A).

Phylogenetic data: Gebhardt *et al.* (2005); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Raffaelea monteteyi* is part of the *R. sulphurea* complex in *Leptographium s.l.*, and is not part of *Raffaelea s.tr.* (De Beer & Wingfield 2012).

Leptographium neomexicanum M.J. Wingf., T.C. Harr. & Crous, Can. J. Bot. 72: 228. 1994 [as *'neomexicanus'*]

Descriptions: Wingfield *et al.* (1994b, pp 228–231, Figs 1–13); Jacobs & Wingfield (2001, pp 124–127, Figs 97–99).

Phylogenetic data: Jacobs *et al.* (2004, 2005, 2006, 2010); Massoumi Alamouti *et al.* (2006); Zhou *et al*. (2008); Paciura *et al.* (2010a); Six *et al*. (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species groups in the *G. wageneri* complex (Six *et al.* 2011; Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Leptographium obscurum (R.W. Davidson) Z.W. de Beer & M.J. Wingf. ***comb. nov.,* MB 801082** ≡ *Ceratostomella obscura* R.W. Davidson, J. Agric. Res. 50: 798. 1935 (basionym) ≡ *Ophiostoma obscurum* (R.W. Davidson) Hendr., Ann. Gembloux 43: 99. 1937 ≡ *Ophiostoma obscurum* (R.W. Davidson) Arx, Antonie van Leeuwenhoek 18: 211. 1952 [*nom. illegit.*, Art. 52.1] ≡ *Ceratocystis obscura* (R.W. Davidson) J. Hunt, Lloydia 19: 30. 1956.

Anamorph: leptographium- to pesotum-like (Davidson 1935, Hunt 1956).

Description: Hunt (1956, pp 11, 30).

Notes: Hunt (1956) stated that perithecia formed in the ex-type culture (CBS 125.39) and compared their morphology with those of *G. olivacea*. Wright & Cain (1961) distinguished *L. obscurum* from *G. sagmatospora* based on ascospore size and *G. olivacea* based on ascospore shape. Upadhyay (1981) suggested *L. obscurum* might be a synonym of *G. sagmatospora*, but did not find the teleomorph on the type specimen and treated it as a doubtful species. The species seems to be distinct, and clearly does not belong in *Ophiostoma* but in *Leptographium s.l.*, although its exact placement should be clarified by sequencing of the ex-type culture. Following the recommendations for nomenclatural stability explained by De Beer & Wingfield (2012), we propose this new combination.

Grosmannia olivacea (Math.) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 91. 2006 ≡ *Ophiostoma olivaceum* Math., Svensk. Bot. Tidskr. 45: 212. 1951 ≡ *Ceratocystis olivacea* (Math.) J. Hunt, Lloydia 19: 29. 1956.

Anamorph: pesotum-like.

Descriptions: Mathiesen (1950, p. 298); Hunt (1956, pp 29–30); Griffin (1968, pp 707–708, Fig. 82 Pl. I); Olchowecki & Reid (1974, p. 1699, Pl. XIII Fig. 262); Upadhyay (1981, p. 52, Figs 116–121); Mouton *et al.* (1993, pp 376–377, Figs 19–22); Romón *et al.* (2007).

Phylogenetic data: Hausner *et al.* (1993b, 2000); Masuya *et al*. (2004); Kim *et al.* (2005b); Greif *et al.* (2006); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: This species groups with five other known species to form the *G. olivacea* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Grosmannia olivaceapini (R.W. Davidson) Z.W. de Beer, Linnakoski & M.J. Wingf., *In* Linnakoski *et al.*, Antonie van Leeuwenhoek 102: 389. 2012 ≡ *Ceratocystis olivaceapini* R.W. Davidson, Mycologia 63: 7. 1971 ≡ *Ophiostoma olivaceapini* (R.W. Davidson) Seifert & G. Okada, *In* Okada *et al.*, Can. J. Bot. 76: 1504. 1998.

Anamorph: pesotum-like.

Descriptions: Upadhyay (1981, p. 54, Figs 122–129); Mouton *et al.* (1993, pp 372–373, Figs 1–4).

Phylogenetic data: Greif *et al.* (2006); Harrington *et al.* (2010); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: This species is part of the *G. olivacea* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012). However, Linnakoski *et al*. (2012) showed that the species boundaries of *G. olivaceapini* and *G. cucullata* are unresolved and that some isolates currently assigned to either of the two species might represent novel cryptic species that should be explored further.

Grosmannia penicillata (Grosmann) Goid., Boll. Staz. Patol. Veg. Roma 15: 156. 1935 ≡ *Leptographium penicillatum* Grosmann, Z. Parasitenk. 3: 94. 1931 ≡ *Ceratostomella penicillata* Grosmann, Hedwigia 72: 190. 1932 ≡ *Scopularia penicillata* (Grosmann) Goid., Boll. Staz. Patol. Veg. Roma 15: 156. 1935 ≡ *Ophiostoma penicillatum* (Grosmann) Siemaszko, Planta Pol. 7: 24. 1939 ≡ *Ceratocystis penicillata* (Grosmann) C. Moreau, Rev. Mycol. (Paris), Suppl. Colon. 17: 22. 1952 ≡ *Verticicladiella penicillata* (Grosmann) W.B. Kendr., Can. J. Bot. 40: 776. 1962.

Anamorph: leptographium-like.

Descriptions: Siemaszko (1939, pp 20, 24–25, Pl. II Figs 1–4); Mathiesen (1950, pp 284–289, Figs 1–2); Davidson (1958, p. 662); Hunt (1956, pp 11, 24–25); Kendrick (1962, pp 776–780, Figs 2–3, 9I-J); Kotýnková-Sychrová (1966, pp 47, 51–52, Fig. 1); Davidson *et al*. (1967, pp 929–930); Griffin (1968, p. 709); Upadhyay (1981, p. 55, Figs 130–137); Solheim (1986, pp 204–205); Yamaoka *et al.* (1997, pp 1223–1224); Jacobs & Wingfield (2001, p.127–131, Figs 100–102).

Phylogenetic data: Hausner *et al.* (1993b, 2000, 2005); Okada *et al.* (1998); Jacobs *et al*. (2001a, d); Masuya *et al*. (2004); Gebhardt *et al.* (2005); Greif *et al.* (2006); Massoumi Alamouti *et al.* (2006, 2007, 2009); Zipfel *et al.* (2006); Mullineux & Hausner (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); Paciura *et al.* (2010a); Mullineux *et al*. (2011); Six *et al.* (2011); Duong *et al*. (2012); Linnakoski *et al.* (2012); De Beer *et al*. (2012); De Beer & Wingfield (2012); Jacobs *et al.* (2012).

Notes: *Grosmannia penicillata* is the type species of *Grosmannia*. Solheim (1986) designated a neotype for this species, which forms a well-supported lineage with 17 other species of *Leptographium s.l.*, designated as the *G. penicillata* complex (Six *et al.* 2011; Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Leptographium peucophilum K. Jacobs & M.J. Wingf., Mycoscience 41: 599. 2000.

Descriptions: Jacobs *et al.* (2000c, pp 599–604, Figs 15–21); Jacobs & Wingfield (2001, pp 131–134, Figs 103–105).

Notes: Teleomorph unknown. *Leptographium peucophilum* resembles *L. procerum* based on morphology (Jacobs *et al.* 2000c; Jacobs & Wingfield 2001), but DNA sequence data is needed to confirm its placement in the *L. procerum* complex.

Grosmannia piceiperda (Rumbold) Goid., Boll. Staz. Patol. Veg. Roma 16: 255. 1936 [as '*piceaperda*'] ≡ *Ceratostomella piceiperda* Rumbold, J. Agric. Res. 52: 436. 1936 [as '*piceaperda*'] ≡ *Ophiostoma piceiperdum* (Rumbold) Arx, Antonie van Leeuwenhoek 18: 211. 1952 [as '*piceaperdum*'] ≡ *Ceratocystis piceiperda* (Rumbold) C. Moreau, Rev. Mycol. (Paris), Suppl. Colon. 17: 22. 1952 [as *'piceaperda*'] ≡ *Leptographium piceiperdum* K. Jacobs, M.J. Wingf. & Crous, Mycol. Res. 104: 240. 2000 [as *'piceaperdum*']

Anamorph: leptographium-like.

Descriptions: Hunt (1956, p. 25); Kotýnková-Sychrová (1966, p. 52); Upadhyay (1981, p. 55, Figs 138–152); Hutchison & Reid (1988, pp 71, 74–75); Jacobs *et al.* (2000b, pp 240–242, Figs 1–11); Jacobs & Wingfield (2001, pp 134–138, Figs 106–108).

Phylogenetic data: Hausner *et al.* (1993a, 2000); Jacobs *et al.* (2001a, d); Gebhardt *et al.* (2004, 2005); Masuya *et al.* (2004, 2005); Kim *et al.* (2005c, d); Massoumi-Alamouti *et al.* (2006, 2007, 2009); Zipfel *et al.* (2006); Mullineux & Hausner (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); Paciura *et al.* (2010a); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: The correction to the epithet, i.e. *piceiperda* and not *piceaperda*, was suggested by Dr Walter Gams. Upadhyay (1981), Hutchison & Reid (1988a), Jacobs *et al.* (2000b), and Jacobs & Wingfield (2001) considered *O. europhioides* a synonym of *O. piceiperdum*, while Harrington (1988) and Hausner *et al.* (1993a, 2000) treated the two species as distinct. Linnakoski *et al*. (2012) and De Beer & Wingfield (2012) suggested that these synonymies are still not settled because isolates labeled as *G. piceiperda* forms at least five lineages, some of which might represent *G. europhioides* or *G. pseudoeurophioides.*

Leptographium pineti K. Jacobs & M.J. Wingf., Mycoscience 41: 596. 2000.

Descriptions: Jacobs *et al.* (2000c, pp 596–599, Figs 1–7); Jacobs & Wingfield (2001, pp 140–143, Figs 112–114).

Phylogenetic data: Jacobs *et al.* (2001d, 2005, 2006, 2010); Kim *et al.* (2004); Zhou *et al*. (2008); Lu *et al.* (2009b); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al*. (2012); De Beer & Wingfield (2012)

Notes: Teleomorph unknown. This species forms a lineage on its own, distinct from other species complexes in *Leptographium s.l.* (Paciura *et al.* 2010a; Six *et al.* 2011; Duong *et al*. 2012; De Beer & Wingfield 2012).

Leptographium pinicola (K. Jacobs & M.J. Wingf.) Z.W. de Beer, Linnakoski & M.J. Wingf., *In* Linnakoski *et al*., Antonie van Leeuwenhoek 102: 389. 2012 ≡ *Hyalorhinocladiella pinicola* K. Jacobs & M.J. Wingf., *In* Jacobs *et al.*, Mycol. Res. 109: 1157. 2005.

Description: Jacobs *et al.* (2005, pp 1157–1158, Figs 19–28).

Phylogenetic data: Jacobs *et al.* (2005); Lu *et al.* (2009a); Paciura *et al*. (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012)

Notes: Teleomorph unknown. This species was described in *Hyalorhinocladiella*, currently treated as a synonym of *Ceratocystiopsis* (De Beer & Wingfield, 2012). It is part of the *L. lundbergii* complex, and was thus transferred to *Leptographium* by Linnakoski *et al*. (2012). The name should not be confused with *O. pinicola* or *C. pinicola*.

Leptographium pini-densiflorae Masuya & M.J. Wingf., Mycoscience 41: 428. 2000.

Descriptions: Masuya *et al.* (2000, pp 426–429, Figs 1–11); Jacobs & Wingfield (2001, pp 138–140, Figs 109–111); Yamaoka *et al.* (2007, p. 101, Figs 1–3).

Phylogenetic data: Jacobs *et al.* (2005, 2006); Kim *et al.* (2005c); Masuya *et al.* (2005); Massoumi Alamouti *et al.* (2006); Zhou *et al*. (2008); Lu *et al.* (2009a, b); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *L. procerum* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Leptographium piriforme Greif, Gibas & Currah, Mycologia 98: 772. 2006.

Descriptions: Greif *et al*. (2006, 772–775, Figs 1–15); Jankowiak & Kolařík (2010, pp 755–756, Fig.1).

Phylogenetic data: Greif *et al.* (2006); Jankowiak & Kolařík (2010); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species groups with *G. crassivaginata* in a distinct lineage in *Leptographium s.l.* (De Beer & Wingfield 2012).

Leptographium pistaciae Paciura, Z.W. de Beer & M.J. Wingf., *In* Paciura *et al.*, Persoonia 25: 104. 2010.

Description: Paciura *et al*. (2010a, p. 104, Figs 6g-l).

Phylogenetic data: Paciura *et al*. (2010a); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Leptographium pistaciae* is part of the *G. penicillata* complex (Paciura *et al*. 2010a; Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Leptographium pityophilum K. Jacobs, M.J. Wingf. & Frisullo, *In* Jacobs *et al.*, Myc. Res. 105: 495. 2001.

Descriptions: Jacobs *et al.* (2001c, pp 495–497, Figs 8–14); Jacobs & Wingfield (2001, pp 143–145, Figs 115–117).

Phylogenetic data: Jacobs *et al.* (2001d); Masuya *et al.* (2004); Massoumi Alamouti *et al.* (2006); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species froups peripherally to the *G. olivacea* complex (Six *et al.* 2011; Duong *et al*. 2012; De Beer & Wingfield 2012).

Leptographium procerum (W.B. Kendr.) M.J. Wingf., Trans. Br. Mycol. Soc. 85: 92. 1985 ≡ *Verticicladiella procera* W.B. Kendr., Can. J. Bot. 40: 783. 1962.

Descriptions: Kendrick (1962, pp 783–786, Fig. 5, 9D–G); Wingfield (1993, p. 46, Fig. 4); Jacobs & Wingfield (2001, pp 144–150, Figs 118–120).

Phylogenetic data: Jacobs *et al.* (2001a, d); Kim *et al.* (2004, 2005a, c, d); Masuya *et al.* (2004); Hausner *et al.* (2005); Greif *et al.* (2006); Massoumi Alamouti *et al.* (2006); Zhou *et al*. (2008); Lu *et al.* (2009a, b); Mullineux & Hausner (2009); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. *Leptographium procerum* groups with eight other species to form the *L. procerum* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Leptographium profanum K. Jacobs, Eckhardt & M.J. Wingf., Can J. Bot. 84: 762. 2006.

Description: Jacobs *et al.* (2006, pp 762–763, Figs 2–9).

Phylogenetic data: Jacobs *et al.* (2006); Zhou *et al*. (2008); Lu *et al.* (2009a, b); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *L. procerum* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Leptographium pruni Masuya & M.J. Wingf., *In* Masuya *et al.*, Mycologia 96: 553. 2004.

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

Phylogenetic data: Masuya *et al.* (2004, 2012); Massoumi Alamouti *et al.* (2006); Matsuda *et al.* (2010); Duong *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species, grouping relatively close to *G. grandifoliae* in *Leptographium s.l.* (Massoumi Alamouti *et al.* (2006); Duong *et al.* 2012; De Beer & Wingfield 2012), is unique in this genus because it produces a sporothrix-like synanamorph (Masuya *et al.* 2004).

Grosmannia pseudoeurophioides (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 91. 2006 ≡ *Ceratocystis pseudoeurophioides* Olchow. & J. Reid, Can. J. Bot. 52: 1700. 1974 ≡ *Ophiostoma pseudoeurophioides* (Olchow. & J. Reid) Hausner, J. Reid & Klassen, Can. J. Bot. 71: 1264. 1993.

Anamorph: leptographium-like (Hausner *et al.* 1993a).

Phylogenetic data: Hausner *et al.* (1993b, 2000); Masuya *et al*. (2004); Mullineux & Hausner (2009); Mullineux *et al*. (2011); De Beer & Wingfield (2012).

Notes: This species was considered a synonym of *G. penicillata* (Upadhyay 1981), of *G. europhioides* (Harrington 1988), and of *G. piceiperda* (Jacobs *et al.* 1998, 2000b, Jacobs & Wingfield 2001). Phylogenetic data of the ex-type isolate by Hausner *et al.* (1993b, 2000), suggested that *G. pseudoeurophioides* is distinct from all three of the above-mentioned species and placed it in the *G. penicillata* complex (De Beer & Wingfield 2012). Based on the distinct ascospore shape (Olchowecki & Reid 1974), the species does not fit with the *G. penicillata* complex, but rather in the *G. piceiperda* complex. De Beer & Wingfield (2012) recommended reconsideration of the species with fresh material and more sequences.

Leptographium pyrinum R.W. Davidson, Mycologia 70: 39. 1978.

Descriptions: Davidson (1978, p. 39, Figs 1, 2, 8); Jacobs & Wingfield (2001, pp 150–152, Figs 121–123).

Phylogenetic data: Jacobs *et al*. (2001d, 2004, 2005, 2006, 2010); Lee *et al.* (2003, 2005); Kim *et al.* (2004, 2005d, c); Lim *et al*. (2004); Masuya *et al.* (2004, 2005); Massoumi Alamouti *et al.* (2006); Zhou *et al*. (2008); Lu *et al.* (2009a, b); Paciura *et al*. (2010a); Roe *et al.* (2010); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. The taxonomy of this species is confused, as reflected by the conflicting sequences from various studies listed above under ‘Phylogenetic data’. Six *et al*. (2011) clarified some of the uncertainties and confirmed that *L. pyrinum* is part of the *G. clavigera* complex, but sequences of more genes are needed to conclusively resolve its status.

Raffaelea quercivora Kubono & Shin. Ito, Mycoscience 43: 256. 2002.
Description: Kubono & Ito (2002, pp 256–259, Figs 1–11).
Phylogenetic data: Kim *et al.* (2009); Seo *et al.* (2010); Matsuda *et al.* (2010); Endoh *et al.* (2011).
Notes: *Raffaealea quercivora* forms part of the *R. sulphurea* complex in *Leptographium s.l.*, and is not part of *Raffaelea s.str.* (De Beer & Wingfield 2012).

Raffaelea quercus-mongolicae K.H. Kim, Y.J. Choi & H.D. Shin, Mycotaxon 110: 193. 2009.
Description: Kim *et al.* (2009, pp 193–195, Fig. 2).
Phylogenetic data: Kim *et al.* (2009); Seo *et al.* (2010).
Notes: Teleomorph unknown. This speices is part of the *R. sulphurea* complex in *Leptographium s.l.*, and is not part of *Raffaelea s.tr.* (De Beer & Wingfield 2012).

Grosmannia radiaticola (J.J. Kim, Seifert & G.H. Kim) Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 91. 2006 ≡ *Ophiostoma radiaticola* J.J. Kim, Seifert & G.H. Kim, Mycotaxon 91: 486. 2005 = *Hyalopesotum pini* L.J. Hutchison & J. Reid, N.Z. J. Bot. 26: 90. 1988 ≡ *Pesotum pini* (L.J. Hutchison & J. Reid) G. Okada & Seifert, Can. J. Bot. 76: 1504. 1998.
Anamorph: pesotum-like.
Descriptions: Hutchison & Reid (1988b, pp 90–91, Figs 32–35, of *Hy. pini*); Kim *et al.* (2005d, pp 486–489, Figs 1–14).
Phylogenetic data: Masuya *et al*. (2004); Kim *et al.* (2005a, d); Thwaites *et al.* (2005); Zipfel *et al.* (2006); Lu *et al.* (2009b); Mullineux & Hausner (2009); Paciura *et al.* (2010a); Six *et al*. (2011); Duong *et al.* (2012); Linnakoski *et al.* (2012); De Beer & Wingfield (2012).
Note: Linnakoski *et al.* (2012) and De Beer & Wingfield (2012) showed that *G. radiaticola* is part of the *G. galeiformis* complex together with two undescribed species.
Thwaites *et al.* (2005) treated *G. radiaticola* as synonym of *G. galeiformis* based on ITS sequences, but Kim *et al.* (2005d) showed with actin and β-tubulin sequences and mating behaviour that the two species are distinct, and that *Hy. pini* is the anamorph of *G. radiaticola*. The name *H. pini* should not to be confused with the anamorph of *O. pini*, treated above as a synonym of *O. minus*.

Leptographium reconditum Jooste, Trans. Br. Mycol. Soc. 70: 154. 1978.
Descriptions: Jooste (1978, pp 152–155, Figs 1–13); Jacobs & Wingfield (2001, pp 152–155, Figs 124–126).
Phylogenetic data: Jacobs *et al.* (2001d, 2004, 2005, 2006, 2010); Kim *et al.* (2004, 2005c, d); Masuya *et al.* (2004); Massoumi Alamouti *et al.* (2006); Zhou *et al*. (2008); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).
Notes: Teleomorph unknown. This species belongs to the *G. wageneri* complex (Six *et al.* 2011; Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Grosmannia robusta (R.C. Rob. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 91. 2006 ≡ *Europhium robustum* R.C. Rob. & R.W. Davidson, *In* Robinson-Jeffrey & Davidson, Can. J. Bot. 46: 1525. 1968 ≡ *Ceratocystis robusta* (R.C. Rob. & R.W. Davidson) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 58. 1981 ≡ *Leptographium robustum* M.J. Wingf., Trans. Br. Mycol. Soc. 85: 92. 1985 ≡ *Ophiostoma robustum* (R.C. Rob. & R.W. Davidson) T.C. Harr., Mycotaxon 28: 42. 1987.

Anamorph: leptographium-like.

Descriptions: Robinson-Jeffrey & Davidson (1968, pp 1525–1526, Figs 10, 11, 12b); Upadhyay (1981, p. 58, Figs 158–162); Jacobs & Wingfield (2001, pp 153–158, Figs 127–129).

Phylogenetic data: Jacobs *et al.* (2001d, 2004, 2005, 2006, 2010); Lee *et al.* (2003, 2005); Lim *et al.* (2004); Kim *et al.* (2005d); Masuya *et al.* (2005); Massoumi Alamouti *et al.* (2006); Zipfel *et al.* (2006); Zhou *et al*. (2008); Lu *et al.* (2009a, b); Matsuda *et al.* (2010); Paciura *et al.* (2010a); Roe *et al.* (2010); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012); Jacobs *et al.* (2012).

Notes: The taxonomy of this species was confused as a consequence of conflicting sequences from various studies listed above. Six *et al*. (2011) clarified the uncertainties and confirmed that it forms part of the *G.clavigera* complex.

Leptographium rostrocylindricum (R.W. Davidson) Z.W. de Beer & M.J. Wingf. ***comb. nov.,*** **MB 801084** ≡ *Ceratostomella rostrocylindrica* R.W. Davidson, Mycologia 34: 658. 1942 (basionym) ≡ *Ophiostoma rostrocylindricum* (R.W. Davidson) Arx, Antonie van Leeuwenhoek 18: 212. 1952 ≡ *Ceratocystis rostrocylindrica* (R.W. Davidson) J. Hunt, Lloydia 19: 26. 1956.

Anamorph: leptographium-like.

Descriptions: Davidson (1942, p. 658, Figs 2B, 3A-E); Hunt (1956, pp 11, 26–27); Upadhyay (1981, p. 59, Figs 163–166).

Notes: In the original description, Davidson (1942) referred to '*Ceratostomella* (*Grosmannia*) *rostrocylindrica'*. He recognised *Ophiostoma*, *Grosmannia* and *Endoconidiophora* (= *Ceratocystis*) as distinct groups, and concluded that, "no doubt the *Leptographium* forms should also constitute a separate genus, as was concluded by Goidànich". Despite this comment, Davidson (1942) treated all these species in *Ceratostomella*. Hunt (1956), Upadhyay (1981) and Harrington (1988) considered *C. rostrocylindrica* a distinct species, but Jacobs & Wingfield (2001) treated it as doubtful because no type material was designated. Hunt (1956) and Upadhyay (1981) referred to an ex-type culture and lectotype (microscope slides) deposited in BPI, which no longer exist. Zipfel *et al.* (2006) did not transfer the species to *Grosmannia* because no DNA sequences or cultures were available. Even in the absence of material, the species is distinct and clearly inappropriately treated in *Ophiostoma*. Based on descriptions of the leptographium-like anamorph and cucullate ascospores in the protologue and by Upadhyay (1981), as well as Davidson's (1942) own treatment of this species in the '*Grosmannia* group', we transfer *Cs. rostrocylindrica* to *Leptographium s.l.* in accordance to the recommendations by De Beer & Wingfield (2012). To confirm the precise placement in a species complex within the genus, neotypification would be necessary (Art. 9.7).

Grosmannia sagmatospora (E.F. Wright & Cain) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 91. 2006 ≡ *Ceratocystis sagmatospora* E.F. Wright & Cain, Can. J. Bot. 39: 1226. 1961 ≡ *Phialographium sagmatosporae* H.P. Upadhyay & W.B. Kendr., Mycologia 66: 183. 1974 ≡ *Ophiostoma sagmatosporum* (E.F. Wright & Cain) H. Solheim, Nord. J. Bot. 6: 203. 1986 [as '*sagmatospora'*] ≡ *Graphium sagmatosporae* (H.P. Upadhyay & W.B. Kendr.) M.J. Wingf. & W.B. Kendr., Mycol. Res. 95: 1332. 1991 ≡ *Pesotum sagmatosporum* (H.P. Upadhyay & W.B. Kendr.) G. Okada & Seifert, *In* Okada *et al.*, Can. J. Bot. 76: 1504. 1998.

Anamorph: pesotum-like.

Descriptions: Griffin (1968, pp 708, 712–713); Olchowecki & Reid (1974, p. 1701, Pl. XIII Figs 254, 257); Upadhyay (1981, p. 60, Figs 167–171); Seifert & Okada (1993, p. 32, Fig. 3E).

Phylogenetic data: Kim *et al.* (2005d); Paciura *et al.* (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: This species groups in the *G. olivacea* complex (Six *et al.* 2011; Linnakoski *et al*. 2012; De Beer & Wingfield 2012).The synnematous anamorph of *G. sagmatospora* is the type species of *Phialographium* (Upadhyay & Kendrick 1974), currently treated as a possible synonym of *Leptographium s. l.*

Grosmannia serpens Goid., Boll. Staz. Patol. Veg. Roma 16: 27. 1936 ≡ *Scopularia serpens* Goid., Boll. Staz. Patol. Veg. Roma 16: 39. 1936 ≡ *Leptographium serpens* (Goid.) Siemaszko, Planta Pol. 7: 34. 1939 ≡ *Ophiostoma serpens* (Goid.) Arx, Antonie van Leeuwenhoek 18: 211. 1952 ≡ *Ceratocystis serpens* (Goid.) C. Moreau, Rev. Mycol. (Paris), Suppl. Colon. 17: 22. 1952 ≡ *Verticicladiella serpens* (Goid.) W.B. Kendr., Can. J. Bot. 40: 781. 1962 ≡ *Leptographium serpens* (Goid.) M.J. Wingf., Trans. Br. Mycol. Soc. 85: 92. 1985 [*nom. illegit.*, Art. 52.1]

Anamorph: leptographium-like.

Descriptions: Goidànich (1937, pp 253–255, Figs 24–25); Siemaszko (1939, p. 34, Pl. V Fig. 3 as *L. serpens*); Hunt (1956, pp 15, 25–26); Kendrick (1962, pp 781–783, Fig. 4, 9H); Kotýnková-Sychrová (1966, pp 47, 52, Fig. 2); Jacobs & Wingfield (2001, pp 157–162, Figs 130–132); Duong *et al.* (2012, pp 722–723, Fig. 5).

Phylogenetic data: Gebhardt *et al.* (2004); Jacobs *et al.* (2004, 2005, 2006, 2010); Kim *et al.* (2005c, 2011); Zipfel *et al.* (2006); Massoumi Alamouti (2006, 2009); Zhou *et al*. (2008); Lu *et al.* (2009b); Mullineux & Hausner (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); Paciura *et al*. (2010a); Six *et al*. (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012); Jacobs *et al.* (2012).

Notes: See discussion under *G. alacris* above.

Leptographium sibiricum K. Jacobs & M.J. Wingf., *In* Jacobs *et al.*, Mycol. Res. 104: 1526. 2000.

Descriptions: Jacobs *et al.* (2000a, pp 1525–1527, Figs 1–9); Jacobs & Wingfield (2001, p.162–164, Figs 133–135).

Phylogenetic data: Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *L. procerum* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Leptographium sinoprocerum Q. Lu, Decock & Maraite, *In* Lu *et al.*, Mycologia 100: 283. 2008.

Description: Lu *et al.* (2008, pp 183–285, Figs 5–17).

Phylogenetic data: Lu *et al.* (2008, 2009a, b); Paciura *et al*. (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This speices is a part of the *L. procerum* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Raffaelea sulphurea (L.R. Batra) T.C. Harr., *In* Harrington *et al*., Mycotaxon 111: 353. 2010 ≡ *Ambrosiella sulphurea* L.R. Batra, Mycologia 59: 992. 1967.

Description: Batra (1967, pp 992–998, Figs 20–21, 26–29).

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 (2012*).*

Notes: Teleomorph unknown. *Raffaelea sulphurea* forms a monophyletic lineage in *Leptographium s.l.* with four other *Raffaelea* spp., and thus is not part of *Raffaelea s.str.* (De Beer & Wingfield 2012).

Leptographium taigense Linnakoski, Z.W. de Beer & M.J. Wingf., *In* Linnakoski *et al*., Antonie van Leeuwenhoek 102: 387. 2012.

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

Phylogenetic data: Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species does not group near any other *Leptographium* species, but is part of *Leptographium s.l.* (Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Leptographium terebrantis S.J. Barras & T.J. Perry, Mycopath. Mycol. Appl. 43: 3. 1971.

Descriptions: Barras & Perry (1971, pp 3–10, Figs 2–7); Jacobs & Wingfield (2001, pp 164–167, Figs 136–138).

Phylogenetic data: Jacobs *et al*. (2001d, 2004); Lee *et al.* (2003, 2005); Six *et al.* (2003, 2011); Kim *et al.* (2004, 2005c, d); Lim *et al.* (2004); Masuya *et al.* (2004, 2005); Hausner *et al.* (2005); Greif *et al.* (2006); Massoumi Alamouti *et al.* (2006, 2009); Zhou *et al*. (2008); Lu *et al*. (2008, 2009a, b); Mullineux & Hausner (2009); Paciura *et al*. (2010a); Roe *et al.* (2010); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. The taxonomy of this species was confused because some sequences listed as *L. terebrantis* in GenBank (Jacobs *et al*. 2001d, 2004; Zhou *et al*. 2008), actually represent *L. procerum*. Also, some reports of *L. terebrantis* (Six *et al*. 2003; Lee *et al.* 2003, 2005; Lim *et al.* 2004; Kim *et al.* 2005c; Massoumi Alamouti *et al.* 2009; Roe *et al.* 2010) actually represent a distinct species, referred to as species X by Six *et al*. (2011), who clarified the taxonomic uncertainties. Species X and the true *L. terebrantis* both form part of the *G. clavigera* complex (Six *et al.* 2011; De Beer & Wingfield (2012).

Leptographium tereforme S. Kim & T.C. Harr., *In* Kim *et al*., Mycologia 103: 156. 2011.
Description: Kim *et al.* (2011, pp 155–158, Fig. 1).

Phylogenetic data: Kim *et al.* (2011); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. Kim *et al*. (2010) based the description of this species on a single ITS sequence without any phylogenetic analyses. De Beer & Wingfield (2012) showed that this sequence groups in the *G. clavigera* complex (Kim *et al*. 2011; De Beer & Wingfield 2012), but sequences of more genes are needed to confirm its status as a distinct species.

Leptographium truncatum (M.J. Wingf. & Marasas) M.J. Wingf., Trans. Br. Mycol. Soc. 85: 92. 1985 ≡ *Verticicladiella truncata* M.J. Wingf. & Marasas, Trans. Br. Mycol. Soc. 80: 232. 1983.

Descriptions: Wingfield & Marasas (1983, pp 232–235, Figs 1–18); Wingfield (1993, p. 46, Fig. 1); Jacobs *et al.* (2005, pp 1155–1156, Figs 14–18).

Phylogenetic data: Hausner *et al.* (2005); Jacobs *et al.* (2005, 2006, 2010); Masuya *et al.* (2005); Zipfel *et al.* (2006); Zhou *et al*. (2008); Lu *et al.* (2009a, b); Mullineux & Hausner (2009); Paciura *et al*. (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. Jacobs & Wingfield (2001) treated *L. truncatum* as synonym of *L. lundbergii*, but Jacobs *et al.* (2005) showed that the two species are distinct. Nevertheless, *L. truncatum* is part of the *L. lundbergii* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Grosmannia truncicola (R.W. Davidson) Z.W. de Beer & M.J. Wingf. ***comb. nov.*, MB 801075** ≡ *Ophiostoma truncicola* R.W. Davidson, Mycologia 47: 63. 1955 (basionym) ≡ *Ceratocystis truncicola* (R.W. Davidson) R.W. Davidson & Aoshima, Ph.D. thesis, University of Tokyo: 7. 1965 [*nom. inval*., Art. 29.1] ≡ *Ceratocystis truncicola* (R.W. Davidson) H.D. Griffin, Can. J. Bot. 46: 710. 1968.

Anamorph: pesotum-like.

Descriptions: Davidson (1955, pp 62–63, Fig. 2); Griffin (1968, pp 710, 713; Fig. 89 Pl. III).

Notes: Upadhyay (1981) and Seifert *et al.* (1993) listed *O. truncicolor* as a synonym of *O. penicillatum*. The species was not included under *O. penicillatum* in the monograph of *Leptographium* (Jacobs & Wingfield 2001), because it has a synnematous anamorph, which distinguishes it from *O. penicillatum*. However, based on the morphology of the sheathed, cucullate ascospores, Griffin (1968) treated this species in the *G. penicillata* complex (as *C. penicillata*). The cleistothecial ascomata resemble those of *G. aurea*, *G. clavigera*, and *G. yunnanensis*, and several *Grosmannia* species (e.g. *G. cainii*, *G. galeiformis*, *G. cucullata*, etc.) also produce synnematous anamorphs. The species is distinct and clearly does not belong in *Ophiostoma s.l.*; even in the absence of DNA sequences, these morphological characters clearly support the placement of this species in *Leptographium s.l.* following the recommendations of De Beer & Wingfield (2012).

Esteya vermicola J.Y. Liou, J.Y. Shih & Tzean, Mycol. Res. 103: 243. 1999.

Description: Liou *et al.* (1999, pp 243–246, Figs 1–10).

Phylogenetic data: Wang *et al.* (2008); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. Although there are similarities between the morphology of *Esteya* and *Leptographium*, the nematophagous ecology of this species and morphology of its infectious conidia are very different from other species of *Leptographium s.l.* It is clear that this species belong in the *Ophiostomatales* and groups in *Leptographium s.l.*, but its generic placement and thus the status of the genus *Esteya* remains unresolved (De Beer & Wingfield 2012).

Leptographium verrucosum (Gebhardt, R. Kirschner & Oberw.) Z.W. de Beer & M.J. Wingf. ***comb. nov.*****, MB 801083** ≡ *Ophiostoma verrucosum* Gebhardt, R. Kirschner & Oberw., Mycol. Progress 1: 378. 2002 (basionym).

Anamorph: hyalorhinocladiella-like*.*

Description: Gebhardt *et al.* (2002, pp 378–381, Figs 1–9).

Phylogenetic data: De Beer & Wingfield (2012).

Notes: Based on LSU sequences, this species can be placed in *Leptographium s.l.*, but not in any particular species complex (De Beer & Wingfield 2012). Its treatment in *Leptographium* rather than *Grosmannia* is based on the recommendations of De Beer & Wingfield (2012).

Grosmannia vesca (R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 92. 2006 ≡ *Ceratocystis vesca* R.W. Davidson, Mycologia 50: 666. 1958 ≡ *Ophiostoma vescum* (R.W. Davidson) Hausner, J. Reid & Klassen. Can. J. Bot. 71: 1264. 1993.

Anamorph: pesotum-like.

Descriptions: Davidson (1958, p. 666); de Hoog & Scheffer (1984, p. 295, Fig. 2); Sameuls (1993, p. 16, Figs 1C–F).

Phylogenetic data: Hausner *et al.* (1992b, 1993a, 2000); Masuya *et al*. (2004); De Beer & Wingfield (2012).

Notes: *Grosmannia vesca* was treated as a synonym of *G. olivacea* (Griffin 1968; Olchowecki & Reid 1974; Upadhyay 1981), but is now considered distinct (Hausner *et al.* 1993a, 2000). De Beer & Wingfield (2012) confirmed its placement in the *G. olivacea* complex.

Grosmannia wageneri (Goheen & F.W. Cobb) Zipfel, Z.W. de Beer & M.J. Wingf., *In* Zipfel *et al.*, Stud. Mycol. 55: 92. 2006 ≡ *Ceratocystis wageneri* Goheen & F.W. Cobb, Phytopathology 68: 1193. 1978 ≡ *Ophiostoma wageneri* (Goheen & F.W. Cobb) T.C. Harr., Mycotaxon 28: 42. 1987 = *Verticicladiella wageneri var. ponderosae* T.C. Harr. & F.W. Cobb, Mycologia 78: 566. 1986 [as '*ponderosa'*] ≡ *Leptographium wageneri var. ponderosae* (T.C. Harr. & F.W. Cobb) T.C. Harr. & F.W. Cobb, Mycotaxon 30: 505. 1987 [as *'ponderosum'*]

Anamorph: leptographium-like.

Descriptions: Goheen & Cobb (1978, pp 1193–1195, Fig. 1); Harrington & Cobb (1986, pp 565–566, Figs 8–10); Harrington & Cobb (1987, pp 502–504); Jacobs & Wingfield (2001, pp 171–174, Figs 142–144).

Phylogenetic data: Jacobs *et al*. (2001d); Masuya *et al.* (2004); Greif *et al.* (2006); Massoumi Alamouti *et al.* (2006); Zipfel *et al.* (2006); Six *et al*. (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph structures for *G. wageneri* were observed only once, associated with *L. wageneri var. ponderosae* (Harrington 1988). Teleomorphs have never been observed for *L. wageneri var. wageneri* or *L. wageneri var. pseudotsugae* (Jacobs & Wingfield 2001; Zipfel *et al.* 2006). *Grosmannia wageneri* groups with five other species to form the *G. wageneri* complex (Linnakoski *et al*. 2012; De Beer & Wingfield 2012).

Leptographium wageneri var. pseudotsugae T.C. Harr. & F.W. Cobb, Mycotaxon 30: 505. 1987.

Descriptions: Harrington & Cobb (1987, pp 502–507, Figs 1–2); Jacobs & Wingfield (2001, pp 174–177, Figs 145–147).

Phylogenetic data: Jacobs *et al.* (2001d); Kim *et al.* (2004, 2005c, d); Masuya *et al.* (2004); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. The taxonomic status of this host-specific variety in the *G. wageneri* complex should be reconsidered using multigene analyses (Witthuhn *et al.* 1997; Linnakoski *et al*. 2012).

Leptographium wageneri (W.B. Kendr.) M.J. Wingf. ***var. wageneri***, Trans. Br. Mycol. Soc. 85: 92. 1985 [as *'Leptographium wageneri'*] ≡ *Verticicladiella wageneri* W.B. Kendr. *var. wageneri*, Can. J. Bot. 40: 793. 1962 [as *'Verticicladiella wagenerii'*]

Descriptions: Kendrick (1962, pp 793–797, Figs 8, 10E-I); Harrington & Cobb (1986, pp 563–565, Figs 2–4); Harrington & Cobb (1987, pp 502–504, Fig. 1); Jacobs & Wingfield (2001, pp 177–179, Figs 148–150).

Phylogenetic data: Jacobs *et al.* (2001d); Masuya *et al.* (2004); Hausner *et al.* (2005); Zipfel *et al.* (2006); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. The taxonomic status of this host-specific variety in the *G. wageneri* complex should be reconsidered using multigene analyses (Witthuhn *et al.* 1997; Linnakoski *et al*. 2012).

Leptographium wingfieldii Morelet, Ann. Soc. Sci. Nat. Arch. Toulon et du Var 40: 43. 1988.

Descriptions: Morelet (1988, pp 43–44); Jacobs & Wingfield (2001, pp 179–182, Fig. 151–153); Jacobs *et al.* (2004, p. 416, Figs 2–7).

Phylogenetic data: Jacobs *et al.* (2001d, 2004, 2005, 2006, 2010); Kim *et al*. (2004, 2005c); Masuya *et al.* (2004, 2005); Hausner *et al.* (2005); Greif *et al.* (2006); Massoumi Alamouti *et al.* (2006); Zhou *et al*. (2008); Lu *et al.* (2009a, b); Mullineux & Hausner (2009); Paciura *et al*. (2010a); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *G. clavigera* complex (Six *et al*. 2011; De Beer & Wingfield 2012).

Leptographium yamaokae T.A. Duong, Z.W. de Beer & M.J. Wingf., *In* Duong *et al.*, Mycologia 104: 725. 2012.

Description: Duong *et al.* (2012, pp 725–726. Fig. 8).

Phylogenetic data: Duong *et al*. (2012); Linnakoski *et al*. (2012); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species is part of the *G. serpens* complex (Duong *et al*. 2012; De Beer & Wingfield 2012).

Grosmannia yunnanensis Yamaoka, Masuya & M.J. Wingf., Mycoscience 49: 235. 2008 ≡ *Leptographium yunnanense* X.D. Zhou, K. Jacobs, M.J. Wingf. & M. Morelet, Mycoscience 41: 576. 2000.

Anamorph: leptographium-like.

Descriptions: Zhou *et al*. (2000, pp 576–577, Figs 1–7); Jacobs & Wingfield (2001, pp 182–185, Figs 154–156); Yamaoka *et al*. (2007, p. 102, Figs 4–6).

Phylogenetic data: Jacobs *et al.* (2004, 2005, 2006, 2010); Kim *et al.* (2005c); Masuya *et al*. (2005, 2012); Massoumi Alamouti *et al.* (2006); Zipfel *et al.* (2006); Zhou *et al*. (2008); Lu *et al.* (2009a, b); Paciura *et al.* (2010a); Roe *et al.* (2010); Six *et al.* (2011); Duong *et al.* (2012); Linnakoski *et al.* (2012); De Beer & Wingfield (2012); Jacobs *et al.* (2012).

Notes: This species groups in the *L. lundbergii* complex (Linnakoski *et al.* 2012; De Beer & Wingfield 2012).

Raffaelea Arx & Hennebert, Mycopathol. Mycol. Appl. 25: 310.1965. emend. T.C. Harr., *In* Harrington *et al.*, Mycotaxon 104: 401. 2008 [type species *R. ambrosiae*]

Notes: We accept the emended description for *Raffaelea* by Harrington *et al.* (2008). De Beer & Wingfield (2012) showed that some species included in *Raffalea* by Harrington *et al*. (2008, 2010) group in the *R. lauricola* and *R. sulphurea* complexes. Those species are excluded from *Raffaelea s.str.* here and are listed under *Ophiostoma s.l.* and *Leptographium s.l.* respectively. One of the species in the *R. sulphurea* complex (*Leptographium s.l.*) is *R. amasae*, the type species of *Dryadomyces*. *Dryadomyces* is thus not a synonym of *Raffaelea* as suggested by Harrington *et al.* (2008, 2010). At present no teleomorphs are known for any species of *Raffaelea*.

Raffaelea albimanens D.B.Scott & J.W. du Toit, Trans. Br. Mycol. Soc. 55: 181. 1970.

Description: Scott & Du Toit (1970, pp 181–182, Fig. 1, Plate 20).

Phylogenetic data: Jones & Blackwell (1998); Gebhardt *et al.* (2005); Kim *et al.* (2009); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species is part of *Raffaelea s.str.* (De Beer & Wingfield 2012).

Raffaelea ambrosiae Arx & Hennebert, Mycopathol. Mycol. Appl. 25: 310.1965.

Descriptions: Von Arx & Hennebert (1965, pp 310–312, Fig. 1); Batra (1967, pp 1011–1013, Figs 35–39).

Phylogenetic data: Jones & Blackwell (1998); Kim *et al.* (2009); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species is part of *Raffaelea s.str.* (De Beer & Wingfield 2012).

Raffaelea arxii D.B. Scott & J.W. du Toit, Trans. Br. Mycol. Soc. 55: 184. 1970.

Description: Scott & Du Toit (1970, pp 184–185, Fig. 3, Plate 20).

Phylogenetic data: Jones & Blackwell (1998); Kim *et al.* (2009); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).

Notes: This species is part of *Raffaelea s.str.* (De Beer & Wingfield 2012).

Raffaelea canadensis L.R. Batra, Mycologia 59: 1010. 1967 ≡ *Tuberculariella ambrosiae* A. Funk, Can. J. Bot. 43: 929. 1965 = *Ambrosiella sulcati* A. Funk, Can. J. Bot. 48: 1445. 1970.

Description: Funk (1965, pp 1445–1447, Figs 1, 3–5, 11, 12).

Phylogenetic data: Cassar & Blackwell (1996); Jones & Blackwell (1998); Rollins *et al.* (2001); Gebhardt *et al.* (2005); Kim *et al.* (2009); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).

Notes: Batra (1967) transferred *T. ambrosiae* to *Raffaelea* but because the name *R. ambrosiae* Arx & Hennebert already existed, he used a new epithet '*canadensis*.' Harrington *et al.* (2010) suggested that *R. sulcati* is a synonym of *R. canadensis*. This species is part of *Raffaelea s. str.* (De Beer & Wingfield 2012).

Raffaelea ellipticospora T.C. Harr., Aghayeva & Fraedrich, Mycotaxon 111: 348. 2010.

Description: Harrington *et al.* (2010, pp 347–348, Figs 3C, 4C, D).

Phylogenetic data: Harrington *et al.* (2010, 2011); De Beer & Wingfield (2012).

Notes: This species is part of *Raffaelea s.str.* (De Beer & Wingfield 2012).

Raffaelea fusca T.C. Harr., Aghayeva & Fraedrich, Mycotaxon 111: 349. 2010.

Description: Harrington *et al.* (2010, pp 347, 349, Figs 3D, 4E, F).

Phylogenetic data: Harrington *et al.* (2010, 2011); De Beer & Wingfield (2012).
Notes: This species is part of *Raffaelea s.str.* (De Beer & Wingfield 2012).

Raffaelea gnathotrichi (L.R. Batra) T.C. Harr., *In* Harrington *et al.*, Mycotaxon 111: 351. 2010 ≡ *Ambrosiella gnathotrichi* L.R. Batra, Mycologia 59: 986. 1967.
Description: Batra (1967, pp 986–990, Figs 4, 5, 8, 9).
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 (2012).
Notes: This species is part of *Raffaelea s.str.* (De Beer & Wingfield 2012).

Raffaelea santoroi Guerrero, Revt. Invest. Agropec. Ser. 5, 3: 100. 1966.
Description: Guerrero (1966, pp 100–102, Figs 1–2).
Phylogenetic data: Jones & Blackwell (1998); Kim *et al.* (2009); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).
Notes: Sutton (1975) did not consider this species appropriately classified in *Raffaelea*, but suggested an affinity with *Sporothrix* based on its catenate conidia. Jones & Blackwell (1998) confirmed that it grouped with other *Raffaelea* spp. in the *Ophiostomatales*, and De Beer & Wingfield (2012) showed it is part of *Raffaelea s.str.*

Raffaelea scolytodis M. Kolařík, Mycol. Res. 113: 50. 2009.
Description: Kolařík & Hulcr (2009, pp 50–56, Figs 5G–K, 7, 9A–C).
Phylogenetic data: Kolařík & Hulcr (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).
Notes: This species is part of *Raffaelea s. str.* (De Beer & Wingfield 2012).

Raffaelea subalba T.C. Harr., Aghayeva & Fraedrich, Mycotaxon 111: 346. 2010.
Description: Harrington *et al.* (2010, pp 346–348, Figs 3B, 4A, B).
Phylogenetic data: Harrington *et al.* (2010); De Beer & Wingfield (2012).
Notes: This species is part of *Raffaelea s.str.* (De Beer & Wingfield 2012).

Raffaelea subfusca T.C. Harr., Aghayeva & Fraedrich, Mycotaxon 111: 349. 2010.
Description: Harrington *et al.* (2010, pp 347–350, Figs 3E, 4G, H).
Phylogenetic data: Harrington *et al.* (2010, 2011); De Beer & Wingfield (2012).
Notes: This species is part of *Raffaelea s.str.* (De Beer & Wingfield 2012).

Raffaelea sulcati A. Funk, Can. J. Bot. 48: 1447. 1970.
Description: Funk (1970, 1447, Figs 2, 6–9, 13, 14).
Phylogenetic data: Jones & Blackwell (1998); Gebhardt *et al.* (2005); Kim *et al.* (2009); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).
Notes: This species is part of *Raffaelea s.str.* (De Beer & Wingfield 2012). The name *R. sulcati* should not be confused with *A. sulcati*, a synonym of *R. canadensis* (see above).

Raffaelea tritirachium L.R. Batra, Mycologia 59: 1013. 1967.
Description: Batra (1967, pp 1013–1014, Fig. 6).
Phylogenetic data: Jones & Blackwell (1998); Kim *et al.* (2009); Massoumi Alamouti *et al.* (2009); Harrington *et al.* (2010); Matsuda *et al.* (2010); De Beer & Wingfield (2012).
Notes: This species is part of *Raffaelea s.str.* (De Beer & Wingfield 2012).

A.2. DISTINCT SPECIES OF UNCERTAIN STATUS (*OPHIOSTOMATALES*)

Ceratocystis acericola H.D. Griffin, Can. J. Bot. 46: 694. 1968.
Anamorph: unknown.

Descriptions: Griffin (1968, pp 694–695, Figs 1–4); Upadhyay (1981, p. 35, Figs 24–25).

Notes: Treated in the Fimbriata Group by Olchowecki & Reid (1974) and Section *Ceratocystis* by Upadhyay (1981), both of which included mixtures of what we now consider *Ceratocystis* and *Leptographium s.l.* species. The morphology of the perithecia and sheathed, orange section shaped ascospores resemble those of some *Ophiostoma* and *Grosmannia* species, rather than *Ceratocystis*. However, the absence of a known anamorph and DNA sequences leaves the correct systematic position of this species uncertain.

Ceratostomella acoma V.V. Miller & Cernzow, Sammlung der Arbeiten des Laboratoriums der Erhaltweg des Holzen, Moscow, p. 123. 1934 ≡ *Ceratocystis acoma* (V.V. Miller & Cernzow) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 21. 1952.

Anamorph: pesotum-like (Moreau 1952).

Description: Potlajczuk & Schekunova (1985, p. 151).

Notes: Material of this species could not be obtained by Hunt (1956). Dr Vadim A. Mel'nik (Komarov Botanical Institute, St. Petersburg, *in litt.* to WDB) confirmed that no material of the species exists in Russian collections. From the description it is clearly a good species of *Ophiostoma* with pesotum-like anamorph and cylindrical ascospores. For an accurate phylogenetic placement, it would be necessary to neotypify and sequence the species (Art. 9.6).

Ceratocystis aequivaginata Olchow. & J. Reid, Can. J. Bot. 52: 1696. 1974.

Anamorph: hyalorhinocladiella-like (Upadhyay 1981).

Description: Upadhyay (1981, p. 36).

Notes: The sheathed ascospores suggest that this species probably belongs to *Leptographium s.l.*, but DNA sequences are needed for an accurate placement.

Ceratocystiopsis alba (DeVay, R.W. Davidson & W.J. Moller) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 120. 1981 ≡ *Ceratocystis alba* DeVay, R.W. Davidson & W.J. Moller, Mycologia 60: 636. 1968.

Anamorph: hyalorhinocladiella-like (Upadhyay 1981).

Description: Upadhyay (1981, p. 120, Figs 428–431).

Phylogenetic data: Hausner *et al.* (1993a).

Note: *Ceratocystiopsis alba* seems to be phylogenetically distantly related to genera in the *Ophiostomatales* (Hausner *et al.* 1993a). The LSU sequence BLASTs closest to *G. abiocarpa* and other *Grosmannia* spp., but with less than 55% similarity. The SSU (V9 region) BLASTs with 94% similarity to *Fragosphaeria reniformis* and *Cop. minuta*, but SSU (V3–V4 regions) show no similarity with any ophiostomatalean fungus, and 97% similarity with *Tricladium* and *Cladosporium* spp. We prefer to treat the species as uncertain until additional sequence data become available. The name should not be confused with *Gr. album* or *S. alba*.

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

Description: de Hoog (1974, pp 22–23, Fig. 7).

Note: Teleomorph unknown. No culture is available for this species. The type specimen, found growing on a *Cordyceps* fruiting body on an insect (de Hoog 1974), should be re-investigated carefully and compared with *Beauveria* and similar entomopathogenic species to confirm its generic placement. The name should not be confused with *Gr. album* or *Cop. alba*.

Ophiostoma brevicolle (R.W. Davidson) de Hoog & R.J. Scheff., Mycologia 76: 297. 1984 ≡ *Ceratocystis brevicollis* R.W. Davidson, Mycologia 50: 667. 1958 ≡ *Leptographium brevicolle* .K. Jacobs & M.J. Wingf., *Leptographium species*, p. 72. 2001.

Anamorph: leptographium-like.

Descriptions: Upadhyay (1981, p. 38, Figs 37–42); de Hoog & Scheffer (1984, p. 295, Fig. 2); Jacobs & Wingfield (2001, pp 72–76, Figs 46–48).

Phylogenetic data: Hausner *et al.* (2000); Jacobs *et al*. (2001d); Masuya *et al*. (2004); Massoumi Alamouti *et al.* (2006); Mullineux & Hausner (2009).

Notes: See the discussion of the contradictory generic placements for *O. brevicolle* based on sequence data by De Beer & Wingfield (2012, as Species 3). Further study is required to establish an accurate generic placement for this species.

Ceratostomella comata V.V. Miller & Cernzow, Sammlung der Arbeiten des Laboratoriums der Erhaltweg des Holzen, Moscow, p. 120. 1934 ≡ *Ceratocystis comata* (V.V. Miller & Cernzow) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 120. 1952.

Anamorph: pesotum-like (Moreau 1952, Hunt 1956).

Description: Potlajczuk & Schekunova (1985, p. 151).

Notes: Material of this species could not be located by Hunt (1956), but he considered the species to be close to *G. olivacea*, *L. obscurum*, and *G. leptographioides*. Dr Vadim A. Mel'nik (Komarov Botanical Institute, St. Petersburg, *in litt.* to WDB) confirmed that no material of this species exists. To make an accurate generic placement, it would be necessary to neotypify and sequence it (Art. 9.6).

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

Description: de Hoog (1974, pp 32–33, Fig. 13).

Notes: Teleomorph unknown. This species contains rhamnose in its cell walls, suggesting a classification in the *Ophiostomatales* (Weijman & de Hoog 1975, 1985), but its generic position needs to be ascertained with DNA sequences.

Ceratostomella defectiva Naumov, J. Petrograd Agron. Inst. 2: 68. 1920 ≡ *Sphaerographium lignicola* Naumov, J. Petrograd Agron. Inst. 2: 68. 1920.

Descriptions: Trotter & Cash (1972, p. 254); Danilova (1979, pp 138–139).

Notes: Although this species is validly described, apparently no material is available. The fact that no asci were observed in the original description, and that it was compared with *O. piliferum* and other species currently treated in *Ophiostoma s.str.* (Naumov 1920), suggests that it probably is a species of *Ophiostoma* as circumscribed here. However, the description is rather vague, so we suggest neotypification (Art. 9.6) and sequencing prior to making a new combination. This is the only Ophiostomatalean species with a reported coelomycetous anamorph, classified in *Sphaerographium*. Verkley (2002) did not examine the type, but excluded the species in his revision of *Sphaerographium,* an anamorph genus that seems to be associated with the *Dermatiaceae, Helotiales* based on rDNA sequences in GenBank.

Ophiostoma deltoideosporum (Olchow. & J. Reid) Hausner, J. Reid & Klassen, Can. J. Bot. 71: 1264. 1993 ≡ *Ceratocystis deltoideospora* Olchow. & J. Reid, Can. J. Bot. 52: 1691. 1974.

Anamorph: hyalorhinocladiella-like.

Description: Upadhyay (1981, p. 77, Figs 253–256).

Phylogenetic data: Hausner *et al.* (1993b); Mullineux & Hausner (2009).

Notes: A short LSU sequence of Hausner *et al.* (1993b), retyped from their publication but not deposited in GenBank, places this species in *Raffaelea s.str.* (De Beer & Wingfield 2012), together with the morphologically similar *O. seticolle*. Similarly, an ITS sequence of *O. deltoideosporum* produced by Mullineux & Hausner (2009) is placed in a lineage with *R. canadensis*, the only species of *Raffaelea s.str*. for which ITS sequence data is currently available publically (De Beer & Wingfield 2012). Together with *O. seticolle*, the generic placement of this species needs to be explored further with more extensive sequencing of more strains.

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

Description: de Hoog (1974, pp 30–31, Fig. 12).

Notes: Teleomorph unknown. The origin of the type culture, recorded as isolated by the multinational company Unilever, is unknown, but the illustrations of the conidiogenous cells of this species by de Hoog (1974) suggest some deviation from the typical morphology for true *Sporothrix* spp. If the culture is still viable, DNA sequences should be determined for it to confirm its generic placement.

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

Anamorph: sporothrix-like.

Phylogenetic data: Villarreal *et al.* (2005); De Beer & Wingfield (2012).

Note: Although Kowalski & Butin (1989) reported two synanamorphs in their cultures of this species, these appear to represent the noncatenate and catenate forms of a sporothrix-like anamorph (Seifert *et al.* 1993). Based on ITS sequences, this species forms a distinct lineage of uncertain generic affiliation in the *Ophiostomatales*, but the sequences donot represent the type (De Beer & Wingfield 2012).

Raffaelea hennebertii D.B. Scott & J.W. du Toit, Trans. Br. Mycol. Soc. 55: 183. 1970.

Description: Scott & Du Toit (1970, pp 183–184, Plate 20).

Phylogenetic data: Jones & Blackwell (1998); Kim *et al.* (2009).

Notes: Teleomorph unknown. Jones & Blackwell (1998) found that the SSU sequence of the ex-type isolate of *R. hennebertii* (CBS 272.70) grouped close to *Melanospora (Melanosporales)*, and although the colony morphology corresponded with the original description, the culture did not sporulate. Presently, the isolate is not listed in the CBS database. If the culture no longer exists, neotypification (Art. 9.6) would be necessary to resolve the generic classification of the species.

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

Description: de Hoog (1974, pp 27–28, Fig. 10).

Notes: Teleomorph unknown. This species was isolated from spider eggs. As with the other reportedly entomopathogenic *Sporothrix* spp., it should be re-investigated carefully and compared with *Beauveria* and similar entomopathogenic species to confirm its generic placement.

Ceratostomella imperfecta V.V. Miller & Cernzow, Sammlung der Arbeiten des Laboratoriums der Erhaltweg des Holzen, Moscow, p. 124. 1934 ≡ *Ceratocystis imperfecta* (V.V. Miller & Cernzow) C. Moreau, Rev. Mycol. (Paris), Suppl. Col. 17: 22. 1952.

Anamorph: leptographium-like (Hunt 1956).

Description: Potlajczuk & Schekunova (1985, p. 152).

Notes: Material of this species could not be obtained by Hunt (1956), but based on the protologue, he suggested that it could be a synonym of *G. penicillata.* Kendrick (1962), Upadhyay (1981) and Harrington (1988) also listed *C. imperfecta* as synonym of *G. penicillata*, apparently based on Hunt's suggestion. The species was not mentioned by Jacobs & Wingfield (2001). Dr Vadim A. Mel'nik (Komarov Botanical Institue, St. Petersburg, *in litt.* to WDB) confirmed that no material of this species exists in Russian collections. To make a new combination, it would be necessary to neotypify (Art. 9.6) and sequence the species.

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

Description: de Hoog (1974, pp 25–26, Fig. 9).

Notes: Teleomorph unknown. This species was isolated from insects. As with the other seemingly entomopathogenic *Sporothrix* spp., it should be re-investigated and compared with *Beauveria* and other entomopathogenic species to determine its generic classification.

Sporothrix isarioides (Petch) de Hoog, Stud. Mycol. 7: 22. 1974 ≡ *Sporotrichum isarioides* Petch, Trans. Br. mycol. Soc. 16: 58. 1931.

Description: de Hoog (1974, pp 23–25, Fig. 8).

Notes: Teleomorph unknown. No culture is available for this species. It was found growing on a *Cordyceps* fruiting body growing on an insect (de Hoog 1974). De Hoog (1974) designated a lectotype and suggested some synonyms not listed here. The lectotype should be re-investigated carefully and compared with *Beauveria* and other entomopathogenic genera to confirm its classification.

Sporothrix lignivora de Mey., Z.W. de Beer & M.J. Wingf., Mycologia 100: 657. 2008.

Description: De Meyer *et al.* (2008, p. 657, Figs 4g-i).

Phylogenetic data: De Meyer *et al.* (2008); De Beer & Wingfield (2012).

Notes: Teleomorph unknown. This species groups in a lineage with some undescribed taxa, distinct from *Ophiostoma s. l.* and was consicered *incertae sedis* in the *Ophiostomatales* by De Beer & Wingfield (2012).

Ceratocystis magnifica H.D. Griffin, Can. J. Bot. 46: 704. 1968.

Anamorph: unknown.

Description: Upadhyay (1981, p. 49, Figs 101–103).

Notes: This species was reated in the Fimbriata Group by Olchowecki & Reid (1974) and Section *Ceratocystis* by Upadhyay (1981), both of which included *Ceratocystis* and *Leptographium s.l.* species. The ascospore shape resembles that of *O. stenoceras*, although they are somewhat smaller in size, suggesting that this might be a species of *Ophiostoma*, rather than a species of *Grosmannia* or *Ceratocystis.* The absence of a known anamorph and the lack of cultures leave the generic classification of this species in question.

Sporothrix ramosissima Arnaud *ex* de Hoog, Stud. Mycol. 7: 28. 1974 ≡ *Gonatobotrys ramosissima* Arnaud, Bull. trimest. Soc. mycol. Fr. 68: 187. 1952 [*nom. inval.*, Art. 36.1]

Description: de Hoog (1974, pp 28–30, Fig. 11).

Notes: Teleomorph unknown. This species was isolated from moist wood and differs morphologically from other *Sporothrix* spp. by branched conidiogenous cells (de Hoog 1974). Only herbarium material exists for this species, which requires more study to confirm its generic placement.

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

Synanamorphs: sporothrix-like and a sporodochial anamorph with septate macroconidia.

Phylogenetic data: Hausner *et al.* (1993b).

Notes: The ex-type isolate of *O. roraimense* (CBS 351.78) does not belong to either the *Ophiostomatales* or *Microascales* based on LSU and SSU data (Hausner *et al.*, 1993b). When the short LSU sequence published for the ex-type isolate (CBS 351.78) was retyped from Hausner *et al.* (1993b, unavailable in GenBank), it BLASTed with high similarity to several *Pseudozyma* isolates (*Ustilaginales*) in GenBank. Furthermore, the sporodochia with septate macroconidia found on the ascomatal wall (Samuels & Müller, 1978) set this species apart from all known *Ophiostoma* species. Until a re-examination of the holotype and/or ex-type culture proves otherwise, we consider the status of this species uncertain.

Ophiostoma seticolle (R.W. Davidson) de Hoog & Scheffer, Mycologia 76: 297. 1984 ≡ *Ceratocystis seticollis* R.W. Davidson, Mycopath. Mycol. Appl. 28: 282. 1966.

Anamorph: hyalorhinocladiella-like.

Descriptions: Olchowecki & Reid (1974, p. 1695); Upadhyay (1981, p. 83, Figs 286–289).

Phylogenetic data: Hausner & Reid (2003); Jacobs *et al.* (2003c).

Notes: The contradictory DNA sequences for this species are discussed as Species 1 by De Beer & Wingfield (2012).

Sporothrix setiphila (Deighton & Piroz.) de Hoog, Stud. Mycol. 7: 32. 1974 ≡ *Calcarisporium setiphilum* Deighton & Piroz., Mycol. Pap. 128: 100. 1972.

Descriptions: Deighton & Pirozynski (1972, pp 100–101, Fig. 52); de Hoog (1974, p. 32).

Notes: Teleomorph unknown. No culture exists for this species, which was found overgrowing a *Meliola* fruiting body (de Hoog 1974). Its type should be compared to other fungicolous *Sporothrix* spp.

Ophiostoma simplex K. Jacobs & M.J. Wingf., *In* Jacobs *et al.*, Mycologia 89: 333. 1997 = *Graphium simplex* K. Jacobs & M.J. Wingf., *In* Jacobs *et al.*, Mycologia 89: 333. 1997.

Anamorph: pesotum-like.

Description: Jacobs *et al.* (1997a, pp 333–337, Figs 1–14).

Notes: The hat-shaped ascospores suggest that this species belongs in *Leptographium* or *Grosmannia*. DNA sequences are needed for an accurate generic placement.

Ceratocystis stenospora H.D. Griffin, Can. J. Bot. 46: 714. 1968.

Anamorph: unknown.

Description: Upadhyay (1981, p. 70, Figs 214–216).

Notes: Neither Griffin (1968) nor Upadhyay (1981) described an anamorph for this species. However, in Fig. 215 (Upadhyay, 1981), a structure resembling a sporothrix-like anamorph with conidia is clearly visible at the apex of a perithecial neck from the type. Griffin (1968) mentioned that the sheathed ascospores resemble those of *O. minus*. It thus seems likely that this species belongs in either *Ophiostoma* or *Leptographium s.l.*, but the type should be re-investigated for confirmation.

Ophiostoma trinacriforme (A.K. Parker) T.C. Harr., Mycotaxon 28: 42. 1987 ≡ *Europhium trinacriforme* A.K. Parker, Can. J. Bot. 35: 175. 1957 ≡ *Ceratocystis trinacriformis* (A.K. Parker) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 63. 1981 ≡ *Leptographium trinacriforme* .K. Jacobs & M.J. Wingf., *Leptographium species*, p. 167. 2001.

Descriptions: Upadhyay (1981, p. 63, Figs 185–190); Jacobs & Wingfield (2001, pp 167–170, Figs 139–141).

Phylogenetic data: Hausner *et al.* (1992b); Hausner *et al.* (2000); Jacobs *et al*. (2001d); Masuya *et al*. (2004); Massoumi Alamouti *et al.* (2006); De Beer *et al*. (2012); De Beer & Wingfield (2012).

Notes: The discrepancies between sequences for this species in the studies of Hausner *et al.* (1992b, 2000) and Jacobs *et al*. (2001d), are discussed in detail by De Beer & Wingfield (2012, as Species 2), who concluded that the generic placement of the species remains uncertain. Because *O. trinacriforme* is the type species of *Europhium* (Parker 1957), these ambiguous results confound a final decision of a synonymy of this genus with either *Ophiostoma* or *Leptographium*.

Ophiostoma valdivianum (Butin) Rulamort, Bull. Soc. Bot. Centre-Ouest, N.S. 17: 192. 1986 [as *'valdiviana'*] ≡ *Ceratocystis valdiviana* Butin, *In* Butin & Aquilar, Phytopathol. Z. 109: 86. 1984 ≡ *Ophiostoma valdivianum* (Butin) T.C. Harr., Mycotaxon 28: 42. 1987 [*nom. illegit.*, Art. 52.1] = *Leptographium valdivianum* Rulamort, Bull. Soc. Bot. Centre-Ouest, N.S. 17: 192. 1986.

Synanamorphs: leptographium- and sporothrix-like.

Notes: Jacobs & Wingfield (2001) considered this a dubious species because no type material or cultures were available. However, an ex-type culture exists (CBS 454.83), and the type was deposited in ZT. The species is probably distinct, but its generic placement should be reconsidered, because it may belong to *Leptographium s.l.*

Raffaelea variabilis B. Sutton, Antonie van Leeuwenhoek 41: 179. 1975.

Description: Sutton (1975, pp 179–181, Fig. 1).

Notes: Teleomorph unknown. This species was isolated from *Lannea grandis* (*Anacardiaceae*), with no reported beetle association (Sutton 1975). Jones & Blackwell

(1998) reported that a SSU sequence supported the classification of this species with other *Raffaelea* spp. in the *Ophiostomatales*. However, the sequence is not in GenBank, and we could not confirm the placement of this species in the *Ophiostomatales*.

A.3. SPECIES NOT VALIDLY PUBLISHED (*OPHIOSTOMATALES*)

Ceratocystis chinensis G.H. Zhao, J. Nanjing Forestry University 16(2): 83. 1992 [*nom. inval.*, Art. 37.1, 37.6]

Anamorph: hyalorhinocladiella-like.

Ophiostoma lignicola G.H. Zhao, J. Nanjing Forestry University 29(3): 117. 2005 [*nom. inval.*, Art. 36.1, 37.1, 37.5]

Anamorph: leptographium-like.

Leptographium galleciae Fern. Magán, Bol. Serv. Plagas 8: 75. 1982 [as '*gallaeciae*'] [*nom. inval*., Art. 36.1, 37.1] ≡ *Leptographium galleciae* Fern. Magán, An. INIA, Ser. Forestal 7: 169. 1983 [as '*gallaeciae*'] [*nom. inval*., Art. 37.1]

Notes: De Ana Magán (1982, 1983) described both a teleomorph and anamorph for *L. galleciae*, but beause they could not induce a teleomorph in cultures, they described the new species in *Leptographium.* Jacobs & Wingfield (2001) suggested a synonymy of *L. galleciae* with *L. serpens*. However, Duong *et al*. (2012) concluded that the descriptions of De Ana Magán (1982, 1983) overlap significantly with the two species of the *G. serpens* complex known from Spain, *G. alacris* and *L. castellanum*; small differences make it impossible to synonymize *L. galleciae* conclusively with either. The name can be validated by precise typification.

Ophiostoma kubanicum Sczerbin-Parfenenko, Rak. Sos. Bol. List. Porod. Moscow, p. 49. 1953 ≡ *Graphium kubanicum* Sczerbin-Parfenenko, Rak. Sos. Bol. List. Porod, Moscow, p. 51. 1953 ≡ *Verticillium kubanicum* Sczerbin-Parfenenko, *ibid.*p. 51. 1953 ≡ *Ceratocystis kubanica* (Sczerbin-Parfenenko) Potlajchuk, Nov. Sist. Niz. Rast. 22: 153. 1985 [*nom. inval*., Art. 36.1]

Synanamorphs: pesotum- and sporothrix-like (Przybyl & de Hoog 1989).

Description: Potlajczuk & Schekunova (1985, p. 153).

Notes: Przybyl & de Hoog (1989) considered this species a possible synonym of *O. piceae*, and Harrington *et al.* (2001) of *O. quercus*, but neither examined authentic material. A culture representing *O. kubanicum* (VKM-F 3181) was a *Fusarium* species (De Beer, unpubl.). Since no other authentic material is available, validation of the species is presently not possible (Grobbelaar *et al*. 2009).

Ceratocystis minor (Hedgc.) J. Hunt ***var. barrasii*** J.J. Taylor, *In* Barras & Taylor, Mycopath. Mycol. Appl. 50: 304. 1973 [*nom. inval.*, Art. 37.1, 37.6]

Notes: Upadhyay (1981) rejected the name because of a lack of ascocarp material, a distinction that is no longer critical as we move away from dual nomenclature. However, Harrington & Zambino (1990) also treated it as a *nomen dubium* and showed that the only existing culture from the original study represented *Cop. ranaculosa*.

Ophiostoma pinicola G.H. Zhao, J. Nanjing Forestry University 29(3): 116. 2005 [*nom. inval*., Art. 36.1, 37.1, 37.6]

Anamorph: Description and figures in protologue not clear.

Notes: The name should not be confused with *Leptographium pinicolum* or *Ceratocystis pinicola*.

Leptographium qinlingensis Tang, *In* Tang *et al.*, Journal of Huazhong Agricultural University 23: 5. 2004 [*nom. inval*., Art. 36.1, 37.1] ≡ *Ophiostoma qinlingensis* Chen & Tang, *In* Tang *et al.*, Journal of Huazhong Agricultural University 23: 5. 2004 [*nom. inval*., Art. 36.1, 37.1]

Notes: This species was isolated from the bark beetle *Dendroctonus armandi* on *Pinus armandi* in China, and its validation should be considered if similar material is obtained from the same vector and host.

B.1. ACCEPTED OPHIOSTOMATOID GENERA AND SPECIES IN THE *MICROASCALES*

Only genera of the three families in the *Microascales* that contain ophiostomatoid species, namely *Ceratocystidaceae*, *Graphiaceae* and *Gondwanamycetaceae* (De Beer *et al*. 2012), are listed here.

Ceratocystis Ellis & Halst., *In* Halsted, Bull. N.J. Agric. Sta. 76: 14. 1890 [type species *C. fimbriata*]
?= *Thielaviopsis* Went, Meded. Proefstn SuikRiet W. Java 5: 4. 1893, emend. A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 69. 2002. Anamorphic synonym. [type species *T. paradoxa*]
?= *Chalaropsis* Peyronel, Staz. Sper. Agr. Ital. 49: 595. 1916. Anamorphic synonym. [type species *Ch. thielavioides*]
?= *Hughesiella* Bat. & A.F. Vital, Anais Soc. Biol. Pernambuco 14: 141. 1956. Anamorphic synonym. [type species *Hu. euricoi*]
= *Rostrella* Zimm., Meded. Lds. Pl. Tuin, Batavia 37: 24. 1900 [*nom. illegit*., Art. 53.1, later homonym for *Rostrella* Fabre, Annls. Sci. Nat., Sér 6, 9: 66. 1879] [type species *Ro. coffeae*]
= *Endoconidiophora* Münch, Naturw. Z. Forst- u. Landw. 6: 564. 1907. Teleomorphic synonym. [type species *En. coerulescens*]
= *Ophiostoma* Syd. section *Longirostrata* Nannf. *pro parte*, *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 407. 1934.
?= *Ambrosiella* Brader *ex* Arx & Hennebert, *Mycopath. Mycol. Appl.* 25: 314. 1965., emend. T.C. Harr., Mycotaxon 111: 354. 2010. Anamorphic synonym. [type species *A. xylebori*]
?= *Phialophoropsis* L.R. Batra, Mycologia 59: 1008. 1967. Anamorphic synonym. [type species *Ph. trypodendri*]
= *Ceratocystis* Ellis & Halst. section *Ceratocystis pro parte*, *In* Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 32. 1981 [type species *C. fimbriata*]
= *Ceratocystis* Ellis & Halst. section *Endoconidiophora* (Münch) H.P. Upadhyay *pro parte*, *In* Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 64. 1981 [type species *C. coerulescens*]

Note: *Ceratocystis s.l.* includes several distinct phylogenetic lineages. Three are well defined and are exemplified by *C. fimbriata*, *C. coerulescens* and *C. moniliformis* (Harrington 2009; B. Wingfield et al. 2012). These lineages are in the process of being accorded generic status (B. Wingfield et al. 2012). This means that species in the *C. coerulescens* and *C. moniliformis* complexes that are now accommodated in *Ceratocystis s.l.* will soon be transferred to new or resurrected genera. All species in the *C. fimbriata* complex will remain in *Ceratocystis* because the genus is typified by *C. fimbriata sensu stricto*. In the current phylogenies some *Ceratocystis* species (e.g. *C. adiposa*, *C. fagacearum*, *C. paradoxa*, and *C. radicicola*) group beyond the three well-resolved complexes (B. Wingfield et al. 2012). These would probably be accommodated in *Ceratocystis* until more data becomes available to resolve their positions.

For a long time, anamorphs of *Ceratocystis* were treated as *Chalara* (Siemaszko 1939; Nag Raj & Kendrick 1975; Upadhyay 1981), until it was shown that the type species of *Chalara* is actually related to the *Helotiales* (Paulin & Harrington 2000; Gernandt *et al.* 2001). Paulin-Mahady *et al.* (2002) amended *Thielaviopsis* to include all chalara-like species with affinities to *Ceratocystis*. They also suggested *Chalaropsis* and *Hughesiella* be treated as synonyms of *Thielaviopsis*. However, species currently treated in *Thielaviopsis* do not form a monophyletic group in *Ceratocystis s.l.* and it is unclear whether this name will be adopted in a single name nomenclature in this family (Harrington 2009; B. Wingfield et al. 2012).

Bakshi (1951) suggested that *Rostrella coffeae* synonymous with *C. fimbriata*, a treatment that has become widely accepted, together with the resulting synonymy of *Rostrella* as a synonym of *Ceratocystis*.

Bakshi (1951) treated *Endoconidiophora* as synonym of *Ceratocystis*, which was widely accepted. The name *Endoconidiophora* could be re-instated to accommodate species in the *C. coerulescens* complex.

The anamorphic ambrosial genus *Ambrosiella* is phylogenetically placed within *Ceratocystis s.l.*, and in common with *Thielaviopsis*, species classified in this genus do not form a monophyletic group (Massoumi Alamouti *et al.* 2009; Six *et al.* 2009; Harrington *et al*. 2010; De Beer *et al.* 2012). The type species for *Phialophoropsis* was transferred to *Ambrosiella* by Harrington *et al.* (2010), implying that this genus should be treated as synonym of *Ambrosiella* (Seifert *et al*. 2011).

Upadhyay (1981) designated formal taxonomic sections within *Ceratocystis*. Although most of the species he included in section *Ceratocystis* are currently treated in *Leptographium s.l.*, three of the species, including *C. fimbriata*, are species of *Ceratocystis s.l.* All the taxa included in his section *Endoconidiophora* are here included in *Ceratocystis s.l.* apart from one species of uncertain status, *C. stenospora*.

The name of the fungal genus *Ceratocystis* should not be confused with *Ceratocystis* Jaekel, a genus of echinoderm fossils (this chapter Table 1; De Beer *et al.* 2012).

Ceratocystis acaciivora Tarigan & M. van Wyk, S. Afr. J. Bot. 77: 301. 2011.

Anamorph: thielaviopsis-like.

Phylogenetic data: Tarigan *et al.* (2011); Kamgan Nkuekam et al. (2012b); Van Wyk *et al*. (2011a).

Notes: This species is a member of the *C. fimbriata* species complex (B. Wingfield et al. 2012).

Ceratocystis adiposa (Butler) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 ≡ *Sphaeronema adiposum* Butler, India Dept. Agric. Mem. Bot. Ser. 1: 40. 1906 ≡ *Ceratostomella adiposa* (Butler) Sartoris, J. Agric. Res. 35: 585. 1927 ≡ *Ophiostoma adiposum* (Butler) Nannf., *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934 ≡ *Endoconidiophora adiposa* (Butler) R.W. Davidson, J. Agric. Res. 50: 802. 1935 = *Ceratostomella major* J.F.H. Beyma, Zbl. Bakt. Parasitkde 2, 91: 348. 1935 ≡ *Ophiostoma majus* (J.F.H. Beyma) Goid., Boll. Staz. Patol. Veg. Roma 15: 158. 1935 ≡ *Ceratocystis major* (J.F.H. Beyma) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.

Anamorph: thielaviopsis-like.

Descriptions: Sartoris (1927, pp 578–585, Figs 1–4); Davidson (1935, pp 801–802); Hunt (1956, pp 10–13); Upadhyay (1981, p. 35, Figs 26–30); Moreau (1952, pp 17–20, Fig. 1); Nag Raj & Kendrick (1975, p.104, 140, Fig. 37).

Phylogenetic data: Hausner *et al.* (1993c); Witthuhn *et al.* (1999); Roux *et al.* (2000); Baker *et al.* (2003); Loppnau & Breuil (2003); Johnson *et al.* (2005); Thorpe *et al.* (2005); Harrington (2009); Kolařík & Hulcr (2009); Massoumi Alamouti *et al.* (2009); Six *et al.* (2009); Sakayaroj *et al.* (2011).

Notes: *Ceratocystis adiposa* groups outside of the three major species complexes defined in *Ceratocystis* (Harrington 2009; B. Wingfield et al. 2012). Hunt (1956), Moreau (1952), Griffin (1968), Olchowecki & Reid (1974), and Nag Raj & Kendrick (1975), all treated *C. major* and *C. adiposa* as distinct. The synonymy of *C. major* with *C. adiposa* was suggested by Upadhyay (1981). Identical SSU sequences for the two species (Hausner *et al.* 1993c) suggest that the synonymy is sound, although sequencing of more variable regions would be advisable to confirm this.

Ceratocystis albifundus M.J. Wingf., De Beer & M.J. Morris, *In* Wingfield *et al.*, Syst. Appl. Microbiol. 19: 196. 1996 [as *'albofundus'*]

Anamorph: thielaviopsis-like.

Phylogenetic data: Wingfield *et al.* (1996); Witthuhn *et al.* (1999); Roux *et al.* (2000, 2004); Barnes *et al.* (2003a, b); Van Wyk *et al.* (2004a, 2007a, b, 2009a, b, 2010, 2011a, b); Kamgan Nkuekam *et al.* (2008a, 2011); Rodas *et al.* (2008); Harrington (2009); Heath *et al.* (2009); Six *et al.* (2009); Tarigan *et al.* (2011).

Notes: This species is a member of the *C. fimbriata* species complex and was the first to be recognized as a discrete taxon in the group (Harrington 2009; B. Wingfield *et al.* 2012).

Ceratocystis atrox M. van Wyk & M.J. Wingf., *In* Van Wyk *et al.*, Australasian Plant Pathol. 36: 411. 2007.

Anamorph: thielaviopsis-like.

Phylogenetic data: Van Wyk *et al*. (2007a, b, 2009a, b, 2010, 2011a, b); Rodas *et al.* (2008); Heath *et al.* (2009); Kamgan Nkuekam *et al*. (2012b); Tarigan *et al.* (2011).

Notes: This species is a member of the *C. fimbriata* species complex (B. Wingfield et al. 2012).

Thielaviopsis australis (Kile) A.E. Paulin, T.C. Harr. & McNew, *In* Paulin-Mahady *et al.*, Mycologia 94: 69. 2002 ≡ *Chalara australis* J. Walker & Kile, *In* Kile & Walker, Austral. J. Bot. 35: 7. 1987.

Anamorph: thielaviopsis-like.

Description: Kile & Walker (1987, pp 7–14, Figs 4–11).

Phylogenetic data: Paulin-Mahady *et al.* (2002); Harrington (2009); Six *et al.* (2009); B. Wingfield *et al.* (2012).

Notes: Teleomorph unknown. This species groups in the *C. coerulescens* complex (Harrington 2009; B. Wingfield et al. 2012).

Thielaviopsis basicola (Berk. & Broome) Ferraris, Fl. ital. crypt. Fungi 1: 233. 1912 ≡ *Torula basicola* Berk. & Broome, Ann. Mag. nat. Hist., Ser. 2 5: 461. 1850 ≡ *Trichocladium basicola* (Berk. & Broome) J.W. Carmich., *In* Carmichael *et al.*, *Genera of Hyphomycetes*, p. 185. 1980 = *Chalara elegans* Nag Raj & W.B. Kendr., *Monogr. Chalara p.* 111. 1975.

Anamorph: thielaviopsis-like.

Description: Nag Raj & Kendrick (1975, pp 108–113, Figs 39–40 as *Ca. elegans*).

Phylogenetic data: Paulin-Mahady *et al.* (2002); Harrington (2009); Heath *et al.* (2009); Six *et al.* (2009); B. Wingfield *et al.* (2012).

Notes: Teleomorph unknown. This species groups with *T. thielavioides* in a clade that is distinct from the major lineages of Ceratocystis (Harrington 2009; B. Wingfield et al. 2012).

Ambrosiella beaveri Six, De Beer & W.D. Stone, *In* Six *et al.*, Antonie van Leeuwenhoek 96: 23. 2009.

Description: Six *et al.* (2009, pp 23–26, Figs 3–5).

Phylogenetic data: Six *et al.* (2009).

Notes: Teleomorph unknown. *Ambrosiella beaveri* groups close to *A. xylebori*, *A. hartigii* and *C. adiposa* outside the major lineages in *Ceratocystis s.l.* (Six *et al.* 2009).

Ceratocystis bhutanensis M. van Wyk, M.J. Wingf. & T. Kirisits, Stud. Mycol. 50: 373. 2004.

Anamorph: thielaviopsis-like.

Phylogenetic data: Van Wyk *et al.* (2004a, 2006a, 2011b); Al-Subhi *et al.* (2006); Kamgan Nkuekam *et al.* (2008a, 2012b); Heath *et al.* (2009); Kolařík & Hulcr (2009); Tarigan *et al.* (2010).

Notes: This species is a member of the *C. moniliformis* species complex (B. Wingfield et al. 2012).

Ceratocystis cacaofunesta Engelbr. & T.C. Harr., Mycologia 97: 64. 2005.

Anamorph: thielaviopsis-like.

Phylogenetic data: Engelbrecht & Harrington (2005); Van Wyk *et al*. (2007a, b, 2009a, b, 2010, 2011a, b); Rodas *et al.* (2008); Harrington (2009); Heath *et al.* (2009); Tarigan *et al.* (2011).

Notes: This is a cryptic species in the *C. fimbriata* species complex (Harrington 2009; B. Wingfield et al. 2012). It was treated as the Latin American 'cacao' population of *C. fimbriata* in earlier studies (Baker Engelbrecht *et al.* 2003).

Ceratocystis caryae J.A. Johnson & T.C. Harr., Mycologia 97: 1086. 2005.

Anamorph: thielaviopsis-like.

Phylogenetic data: Johnson *et al.* (2005); Van Wyk *et al*. (2007a, b, 2009a, b, 2010, 2011a, b); Rodas *et al.* (2008); Harrington (2009); Heath *et al.* (2009); Kamgan Nkuekam *et al*. (2012b); Tarigan *et al.* (2011).

Notes: This species is a member of the *C. fimbriata* species complex (Harrington 2009; B. Wingfield et al. 2012).

Thielaviopsis ceramica R.N. Heath & Jol. Roux, *In* Heath *et al.*, Fungal Diversity 34: 60.

Phylogenetic data: Heath *et al.* (2009); Van Wyk *et al*. (2011b).

Notes: Teleomorph unknown. This species is a member of the *C. moniliformis* species complex (Heath *et al.* 2009).

Ceratocystis coerulescens (Münch) Bakshi, Trans. Br. Mycol. Soc. 33: 114. 1950. emend. T.C. Harr. & M.J. Wingf., Can. J. Bot. 76: 1448. 1998 ≡ *Endoconidiophora coerulescens* Münch, Naturw. Z. Land. Forstw. 5: 564. 1907 ≡ *Ophiostoma coerulescens* (Münch) Nannf., *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934 = *Chalara ungeri* Sacc., Syll. Fung. 4: 336. 1886 ≡ *Thielaviopsis ungeri* (Sacc.) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 70. 2002.

Anamorph: thielaviopsis-like.

Descriptions: Lagerberg *et al*. (1927, pp 196–203, Figs 22–26); Davidson (1935, pp 798–799); Siemaszko (1939, pp 20–22, Pl. I Figs 9–13); Bakshi (1951, pp 2–5); Hunt (1956, pp 17, 21–23); Griffin (1968, pp 700–701); Nag Raj & Kendrick (1975, pp 94, 138–139, Fig. 32B); Upadhyay (1981, p. 65, Figs 191–196); Potlajczuk & Schekunova (1985, pp 149–150); Harrington & Wingfield (1998, pp 1448–1449).

Phylogenetic data: Hausner *et al.* (1993c); Witthuhn *et al.* (1998, 2000); Roux *et al.* (2000); Paulin-Mahady *et al.* (2002); Barnes *et al.* (2003a, b); Loppnau & Breuil (2003); Harrington (2009); Kolařík & Hulcr (2009); Massoumi Alamouti *et al.* (2009); Six *et al.* (2009); B. Wingfield *et al*. (2012).

Notes: Harrington & Wingfield (1998) designated a neotype for *C. coerulescens*, while Nag Raj & Kendrick (1975) did the same for *Ca. ungeri*. Nag Raj & Kendrick (1975) accepted the suggestion by Münch (1907) that *Ca. ungeri* represented the anamorph of *C. coerulescens*. Witthuhn *et al.* (1998) showed that isolates identified as *C. coerulescens* formed three distinct clades based on ITS data. These were later described as *C. coerulescens sensu stricto*, *C. pinicola*, and *C. resinifera* (Harrington & Wingfield 1998). *Ceratocystis coerulescens* is the type species of *Endoconiophora* and exemplifies the *C. coerulescens* species complex, for which the name *Endoconiophora* will probably be re-instated (Harrington 2009; B. Wingfield et al. 2012).

Ceratocystis colombiana M. van Wyk & M.J. Wingf., Fungal Diveristy 40: 111. 2010.

Anamorph: thielaviopsis-like.

Phylogenetic data: Van Wyk *et al.* (2010, 2011a, b); Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2011).

Notes: This species is a member of the *C. fimbriata* species complex (B. Wingfield *et al.* 2012).

Ceratocystis corymbiicola Kamgan & Jol. Roux, *In* Kamgan Nkuekam *et al*., Antonie van Leeuwenhoek 101: 237. 2012.

Anamorph: thielaviopsis-like.

Phylogenetic data: Kamgan Nkuekam *et al.* (2012b).

Notes: This species is a member of the *C. fimbriata* species complex (Kamgan Nkuekam *et al.* 2012b).

Ceratocystis curvata M. van Wyk & M.J. Wingf., Fungal Diversity 46: 122. 2011.

Anamorph: thielaviopsis-like.

Phylogenetic data: Van Wyk *et al.* (2011a, b).

Notes: This species is a member of the *C. fimbriata* species complex (Van Wyk *et al.* 2011b).

Ceratocystis diversiconidia M. van Wyk & M.J. Wingf., Fungal Diversity 46: 125. 2011.

Anamorph: thielaviopsis-like.

Phylogenetic data: Van Wyk *et al.* (2011a, b).

Notes: This species is a member of the *C. fimbriata* species complex (Van Wyk *et al.* 2011b).

Ceratocystis douglasii (R.W. Davidson) M.J. Wingf. & T.C. Harr., *In* Wingfield *et al.*, Can. J. Bot. 75: 832. 1997 ≡ *Endoconidiophora coerulescens* f. *douglasii* R.W. Davidson, Mycologia 45: 584. 1953.

Anamorph: thielaviopsis-like.

Phylogenetic data: Witthuhn *et al.* (1998, 2000); Barnes *et al.* (2003a); Loppnau & Breuil (2003); Harrington (2009); Kolařík & Hulcr (2009); Six *et al.* (2009).

Notes: *Endoconidiophora coerulescens* f. *douglasii* was considered a synonym of *C. coerulescens* by Upadhyay (1981). Wingfield *et al.* (1997) showed *C. douglasii* is distinct and elevated it to species level. It is now considered as a member of the *C. coerulescens* species complex (Harrington 2009; B. Wingfield et al. 2012). The name should not be confused with *Leptographium douglasii*.

Ceratocystis ecuadoriana M. van Wyk & M.J. Wingf., Fungal Diversity 46: 122. 2011.

Anamorph: thielaviopsis-like.

Phylogenetic data: Van Wyk *et al.* (2011a, b).

Notes: This species is a member of the *C. fimbriata* species complex (Van Wyk *et al.* 2011b).

Ceratocystis erinaceus Bohár, Acta Phytopathologica et Entomologica Hungarica 31: 215. 1996.

Anamorph: thielaviopsis-like.

Notes: The morphology described in the protologue suggests that this species might be a member of the *C. coerulescens* complex.

Ceratocystis eucalypti Z.Q. Yuan & Kile, *In* Kile *et al.*, Mycol. Res. 100: 573. 1996 ≡ *Chalara eucalypti* Z.Q. Yuan & Kile, *In* Kile *et al.*, Mycol. Res. 100: 573. 1996 ≡ *Thielaviopsis eucalypti* (Z.Q. Yuan & Kile) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 69. 2002.

Anamorph: thielaviopsis-like.

Description: Kile *et al.* (1996, pp 573–575, Figs 1–8).

Phylogenetic data: Witthuhn *et al.* (1998, 2000); Roux *et al.* (2000); Barnes *et al.* (2003a, b); Paulin-Mahady *et al.* (2002); Harrington (2009); Six *et al.* (2009); B. Wingfield *et al.* (2012).

Notes: This is a member of the *C. coerulescens* species complex (Harrington 2009; B. Wingfield et al. 2012).

Thielaviopsis euricoi (Bat. & A.F. Vital) A.E. Paulin, T.C. Harr. & McNew, *In* Paulin-Mahady *et al.*, Mycologia 94: 70. 2002 ≡ *Hughesiella euricoi* Bat. & A.F. Vital, Anais Soc. Biol. Pernambuco 14: 142. 1956.

Phylogenetic data: Paulin-Mahady *et al.* (2002); Harrington (2009); B. Wingfield *et al.* (2012).

Notes: Teleomorph unknown. This species is the type species of the genus *Hughesiella* and groups in the *C. paradoxa* complex (Harrington 2009).

Ceratocystis fagacearum (Bretz) J. Hunt, Lloydia 19: 21. 1956 ≡ *Endoconidiophora fagacearum* Bretz, Phytopathology 42: 437. 1952 = *Chalara quercina* Henry, Phytopathology 34: 631. 1944 ≡ *Thielaviopsis quercina* (Henry) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 70. 2002.

Anamorph: thielaviopsis-like.

Descriptions: Hunt (1956, p. 21); Nag Raj & Kendrick (1975, pp 94, 131, Fig. 32A); Upadhyay (1981, p. 66); Potlajczuk & Schekunova (1985, p. 150); Kolařík & Hulcr (2009).

Phylogenetic data: Hausner *et al.* (1993c); Witthuhn *et al.* (1999); Roux *et al.* (2000); Paulin-Mahady *et al.* (2002); Barnes *et al.* (2003b); Masuya *et al.* (2004); Jensen-Tracy *et al*. (2009); Harrington (2009); Six *et al.* (2009); B. Wingfield *et al.* (2012).

Notes: *Ceratocystis fagacearum* groups outside the three major species complexes defined by B. Wingfield *et al.* (2012), but close to *A. ferruginea* (Harrington 2009; Six *et al.* 2009).

Ambrosiella ferruginea L.R. Batra, Mycologia 59: 980. 1967 ≡ *Monilia ferruginea* Math.-Käärik, Medd. Skogsforskninginst. 43: 57. 1953 [*nom. illegit.*, Art. 53.1, *non M. ferruginea* Pers. 1822]

Descriptions: Mathiesen-Käärik (1953, pp 53–57, Figs 5–7); Batra (1967, pp 1000–1004, Figs 30, 31, 40).

Phylogenetic data: Cassar & Blackwell (1996); Rollins *et al.* (2001); Paulin-Mahady *et al*. (2002); Gebhardt *et al.* (2005); Harrington (2009); Massoumi Alamouti *et al.* (2009); Six *et al.* (2009); Matsuda *et al.* (2010).

Notes: Teleomorph unknown. This species does not group in the same lineage as *A. xylebori* and its relatives in *Ceratocystis s.l.*, and also has a different β-tubulin intron arrangement than these species (Massoumi Alamouti *et al.* 2009, Six *et al.* 2009*).*

Ceratocystis ficicola Kajitani & Masuya, Mycoscience 52: 351. 2011.

Anamorph: thielaviopsis-like.

Phylogenetic data: Kajitani & Masuya (2011).

Notes: This species is a member of the *C. fimbriata* species complex (Kajitani & Masuya 2011).

Ceratocystis fimbriata Ellis & Halst., *In* Halsted, Bull. N.J. Agric. Sta. 76: 14. 1890 ≡ *Sphaeronaema fimbriatum* (Ellis & Halst.) Sacc., Syll. Fung. 10: 125. 1892 ≡ *Ceratostomella fimbriata* (Ellis & Halst.) Elliott, Phytopathology 13: 56. 1923 ≡ *Ophiostoma fimbriatum* (Ellis & Halst.) Nannf., *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934 ≡ *Endoconidiophora fimbriata* (Ellis & Halst.) R.W. Davidson, J. Agric. Res. 50: 800. 1935 = *Rostrella coffeae* Zimm., Medded. s'Lands Plantentuin 37: 32. 1900 ≡ *Ophiostoma coffeae* (Zimm.) Arx, Antonie van Leeuwenhoek 18: 210. 1952 ≡ *Ceratocystis moniliformis f. coffeae* (Zimm.) C. Moreau, Bull. Sci., Minist. Fr. D'outre mer 5: 424. 1954.

Anamorph: thielaviopsis-like.

Descriptions: Davidson (1935, pp 799–800); Hunt (1956, pp 11–16); Webster & Butler (1967, pp 1459–1463, Pl. I-VI); Griffin (1968, p. 703); Morgan-Jones (1967a, Figs A-G); Olchowecki & Reid (1974, p. 1699, Pl. XIII Fig. 258); Matsushima (1975, p. 169, Pl. 382 & 383); Nag Raj & Kendrick (1975, pp 118, 141, Fig. 45); Upadhyay (1981, p. 44, Figs 69–72); Potlajczuk & Schekunova (1985, p. 150); Engelbrecht & Harrington (2005, pp 63–64).

Phylogenetic data: Hausner *et al.* (1992b, 1993a, c); Wingfield *et al.* (1996); Witthuhn *et al.* (1998, 1999, 2000); Réblová & Winka (2000); Roux *et al.* (2000, 2004); Baker *et al.* (2003); Barnes *et al.* (2003a, b); Marin *et al.* (2003); Hausner & Reid (2004); Van Wyk *et al.* (2004b, 2007a, b, 2009a, b, 2010, 2011a, b); Johnson *et al.* (2005); Thorpe *et al.* (2005); Schoch *et al.* (2007); Kamgan Nkuekam *et al.* (2008a, 2011); Rodas *et al.* (2008); Harrington (2009); Heath *et al.* (2009); Kolařík & Hulcr (2009); Six *et al.* (2009); Matsuda *et al.* (2010); Sakayaroj *et al.* (2011); Tarigan *et al.* (2011); B. Wingfield *et al.* (2012).

Note: *Ceratocystis fimbriata* is the type species of the genus, and the nominal species of the *C. fimbriata* species complex. Pontis (1951) considered *R. coffeae* a synonym of *C. fimbriata*, although he noted biological differences between the sweet potato and coffee tree isolates. Recent studies distinguished between geographical and host specific populations, including populations from coffee, in the *C. fimbriata* species complex, based on DNA sequence comparisons for multiple gene regions (Harrington 2000; Barnes *et al.* 2001, 2003b; Baker *et al.* 2003; Marin *et al.* 2003; Engelbrecht *et al.* 2004; Steimel *et al.* 2004; Johnson *et al.* 2005). Van Wyk *et al.* (2010) described two of these host specific groups as new species from coffee in Colombia, but did consider the possibility that one of them might represent *R. coffeae*, probably because the latter was originally described from coffee in Java (Indonesia). For the time being, we treat *R. coffeae* as a synonym of *C. fimbriata*, until future studies with fresh isolates from coffee in Java provide more insight.

Microsatellite markers were developed for the exploration of population diversity within *C. fimbriata* (Rizatto *et al*. 2010).

Ceratocystis fimbriatomima M. van Wyk & M.J. Wingf., Fungal Diversity 34: 180. 2009.

Anamorph: thielaviopsis-like.

Phylogenetic data: Van Wyk *et al.* (2009a, 2010, 2011a, b); Kamgan Nkuekam *et al*. (2012b); Tarigan *et al.* (2011).

Notes: This species is a member of the *C. fimbriata* species complex (B. Wingfield et al. 2012).

Ceratocystis fujiensis M.J. Wingf., Yamaoka & Marin, *In* Marin *et al.*, Mycol. Res. 109: 1142. 2005.

Anamorph: thielaviopsis-like.

Phylogenetic data: Marin *et al.* (2005); Kolařík & Hulcr (2009).

Notes: *Ceratocystis fujiensis* is a member of the *C. coerulescens* species complex (B. Wingfield *et al.* 2012).

Ceratocystis harringtonii Z.W. de Beer & M.J. Wingf. **nom. nov., MB 801067** ≡ *Ceratocystis populicola* J.A. Johnson & T.C. Harr., Mycologia 97: 1084. 2005 [*nom. illegit*., Art 53.1]

Anamorph: thielaviopsis-like.

Phylogenetic data: Johnson *et al.* (2005); Van Wyk *et al.* (2007a, b, 2009a, b, 2010, 2011b); Rodas *et al.* (2008); Harrington (2009); Heath *et al.* (2009); Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2011).

Notes: This species was validly published by Johnson *et al.* (2005), but the name was a later homonym for *Ceratocystis populicola* Olchow. & J. Reid (= *Ophiostoma populicola*) and, therefore, illegitimate. We thus provided it with a new, legitimate name here. It is a member of the *C. fimbriata* species complex (Harrington 2009; B. Wingfield *et al.* 2012).

Ambrosiella hartigii L.R. Batra, Mycologia 59: 998. 1967.

Description: Batra (1967, pp 997–1000, Figs 12, 13, 32–34).

Phylogenetic data: Cassar & Blackwell (1996); Rollins *et al.* (2001); Paulin-Mahady *et al.* (2002); Gebhardt *et al.* (2005); Harrington (2009); Massoumi Alamouti *et al.* (2009); Matsuda *et al.* (2010); Six *et al.* (2009).

Notes: Teleomorph unknown. This species groups with *A. xylebori* and *A. beaveri* in a distinct lineage in *Ceratocystis s.l.*, and has the same β-tubulin intron arrangement than these two species (Six *et al.* 2009).

Ceratocystis inquinans Tarigan, M. van Wyk & M.J. Wingf., Mycoscience 51: 58. 2010.
Anamorph: thielaviopsis-like.
Phylogenetic data: Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2010).
Notes: This species is a member of the *C. moniliformis* species complex (B. Wingfield *et al.* 2012).

Ceratocystis laricicola Redfern & Minter, *In* Redfern *et al.*, Plant Pathol. 36: 468. 1987.
Anamorph: thielaviopsis-like.
Descriptions: Harrington & Wingfield (1998, pp 1453, 1456); Yamaoka *et al.* (1998, pp 369–371, Figs 6–10); Marin *et al.* (2005, pp 1142, 1144).
Phylogenetic data: Witthuhn *et al.* (1998, 1999, 2000); Barnes *et al.* (2003a); Marin *et al.* (2005); Harrington (2009); Six *et al.* (2009).
Notes: *Ceratocystis laricicola* was distinguished from the morphologically similar *C. polonica* by Witthuhn *et al.* (2000) and Harrington *et al.* (2002) by the different bark beetle associate and conifer host. This species is a member of the *C. coerulescens* species complex (Harrington 2009; B. Wingfield *et al.* 2012).

Ceratocystis larium M. van Wyk & M.J. Wingf., Persoonia 22: 80. 2009.
Anamorph: thielaviopsis-like.
Description and *Phylogenetic data*: Van Wyk *et al.* (2009a, 2011a).
Notes: This species is a member of the *C. fimbriata* species complex (B. Wingfield *et al.* 2012).

Ceratocystis mangicola M. van Wyk & M.J. Wingf., *In* Van Wyk *et al.*, Mycotaxon 117: 395. 2011.
Anamorph: thielaviopsis-like.
Phylogenetic data: Van Wyk *et al.* (2011a).
Notes: This species is a member of the *C. fimbriata* species complex (Van Wyk *et al.* 2011a).

Ceratocystis manginecans M. van Wyk, Al Adawi & M.J. Wingf., *In* Van Wyk *et al.*, Fungal Diversity 27: 224. 2007.
Anamorph: thielaviopsis-like.
Phylogenetic data: Van Wyk *et al.* (2007a, 2009a, b, 2010, 2011a, b); Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2011).
Notes: This species is a member of the *C. fimbriata* species complex (B. Wingfield *et al.* 2012).

Ceratocystis mangivora M. van Wyk & M.J. Wingf., *In* Van Wyk *et al.*, Mycotaxon 117: 397. 2011.
Anamorph: thielaviopsis-like.
Phylogenetic data: Van Wyk *et al.* (2011a).
Notes: This species is a member of the *C. fimbriata* species complex (Van Wyk *et al.* 2011a).

Ceratocystis microbasis Tarigan, M. van Wyk & M.J. Wingf., Mycoscience 51: 61. 2010.
Anamorph: thielaviopsis-like.
Phylogenetic data: Tarigan *et al.* (2010); Kamgan Nkuekam *et al.* (2012b).
Notes: This species is a member of the *C. moniliformis* species complex (B. Wingfield *et al.* 2012).

Ceratocystis moniliformis (Hedgc.) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 ≡ *Ceratostomella moniliformis* Hedgc., Mo. Bot. Gard. Ann. Rep. 17: 78. 1906 ≡ *Ophiostoma moniliforme* (Hedgc.) Syd., *In* Sydow & Sydow, Annls mycol. 17: 43. 1919 ≡ *Endoconidiophora moniliformis* (Hedgc.) R.W. Davidson, J. Agric. Res. 50: 800. 1935 ≡ *Ceratocystis moniliformis* (Hedgc.) M. Moreau & Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 141. 1952 [*nom. illegit.*, Art. 52.1] = *Endoconidiophora bunae* Kitajima, Bull. Imp. For. Exp. Sta., Meguro, Tokyo 35: 126. 1936 ≡ *Ophiostoma bunae* (Kitajima) Arx, Antonie van Leeuwenhoek 18: 211. 1952 [as *'lunae*'] ≡ *Ceratocystis bunae* (Kitajima) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 = *Ceratocystis wilsonii* Bakshi, Mycol. Pap. 35: 8. 1951 [as *'wilsoni'*] ≡ *Ceratocystis moniliformis* f. *wilsonii* C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 23. 1952 [as *'wilsoni'*; *nom. inval*., Art. 36.1] = *Ophiostoma moniliforme* f. *davidsonii* Luc, Rev. Mycol. (Paris) Suppl. Col. 17: 12. 1952 [*nom. inval*., Art. 36.1] = *Ophiostoma moniliforme* f. *pycnanthi* Luc, Rev. Mycol. (Paris) Suppl. Col. 17: 12. 1952 [*nom. inval*., Art. 36.1] = *Ophiostoma moniliforme* f. *typica* Luc, Rev. Mycol. (Paris) Suppl. Col. 17: 12. 1952 [*nom. inval*., Art. 24.3 & 36.1] = *Ophiostoma moniliforme* f. *theobromae* Luc, Rev. Mycol. (Paris) Suppl. Col. 17: 13. 1952 [*nom. inval*., Art. 36.1] = *Ceratocystis filiformis* Roldan, Philip. J. Sci. 91: 418. 1962.

Anamorph: thielaviopsis-like.

Descriptions: Hedgcock (1906, pp 78–80, Pl. 3 Fig. 5, Pl. 5 Figs 3–5); Davidson (1935, pp 799–800); Moreau & Moreau (1952, Figs 1–4); Luc (1952, p.12–15, Figs 1–2); Hunt (1956, pp 13, 17–19); Morgan-Jones (1967b, Figs A-H); Nag Raj & Kendrick (1975, pp 116, 141–142, Fig. 43A); Upadhyay (1981, p. 51, Figs 109–115); Maekawa *et al.* (1987, pp 8–10, Figs 7–18); Kowalski & Butin (1989, pp 238–241).

Phylogenetic data: Hausner *et al.* (1992b; 1993c); Witthuhn *et al.* (1999); Barnes *et al.* (2003a, b); Hausner & Reid (2004); Masuya *et al.* (2004); Roux *et al.* (2004); Van Wyk *et al.* (2004a, 2006, 2011b); Al-Subhi *et al.* (2006); Kamgan Nkuekam *et al.* (2008a, 2012b); Harrington (2009); Heath *et al.* (2009); Kolařík & Hulcr (2009); Massoumi Alamouti *et al.* (2009); Six *et al.* (2009); Tarigan *et al.* (2010).

Notes: Luc (1952) invalidly described four varieties of *C. moniliformis*. Moreau (1952) reduced a further two species, *C. wilsonii* and *C. variospora* (now considered a distinct species), to *formae* of *C. moniliformis*, and treated *R. coffeae* as a synonym (see above under *C. fimbriata*). Moreau & Moreau (1952) synonymised *O. moniliforme* f. *theobromae*, and Hunt (1956) *E. bunae* and *C. wilsonii*, with *C. moniliformis*. Nag Raj & Kendrick (1975) and Upadhyay (1981) listed *C. filiformis* as synonym of *C. moniliformis*. The tenability of all these synonyms should be carefully reconsidered with DNA sequence data and fresh isolates. *Ceratocystis moniliformis* defines a discrete group of cryptic species in *Ceratocystis sensu lato* that will assume generic status (B. Wingfield *et al.* 2012).

Ceratocystis moniliformopsis Yuan & Mohammed, Austral. Syst. Bot. 15: 126. 2002.

Anamorph: thielaviopsis-like.

Phylogenetic data: Van Wyk *et al.* (2004b, 2006, 2011b); Al-Subhi *et al.* (2006); Kamgan Nkuekam *et al.* (2008a, 2012b); Harrington (2009); Heath *et al.* (2009); Tarigan *et al.* (2010).

Notes: This is a member of the *C. moniliformis* species complex (Harrington 2009; B. Wingfield *et al.* 2012).

Ceratocystis musarum Riedl, Sydowia 15: 248. 1962 ≡ *Thielaviopsis paradoxa* (De Seynes) Höhn. *var. musarum* R.S. Mitchell, J. Coun. Sci. Ind. Res. Australia, 10: 130. 1937 [*nom. inval.*, Art. 36.1] ≡ *Thielaviopsis musarum* (R.S. Mitchell) Riedl, Sydowia 15: 249. 1962.

Anamorph: thielaviopsis-like.

Phylogenetic data: Harrington (unpublished in GenBank).

Notes: Upadhyay (1981) proposed *C. musarum* as a synonym of *C. paradoxa*, but Harrington (2009) included an EF-1α sequence (HM569629) for an isolate (C1753), presumably from banana and labelled as '*C. musarum*', in his analyses. The sequence differs substantially from other *C. paradoxa* sequences, suggesting that it is a distinct species in the *C. paradoxa* clade (Harrington 2009).

Ceratocystis neglecta M. van Wyk, Jol. Roux & C. Rodas, *In* Rodas *et al.*, Fungal Diversity 28: 80. 2008.

Anamorph: thielaviopsis-like.

Phylogenetic data: Rodas *et al.* (2008); Van Wyk *et al.* (2009a, 2010, 2011a, b); Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2011).

Notes: This species is a member of the *C. fimbriata* species complex (B. Wingfield *et al.* 2012). The name should not to be confused with *Cop. neglecta*.

Thielaviopsis neocaledoniae (Kiffer & Delon) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 70. 2002 ≡ *Chalara neocaledoniae* Dadant *ex* Kiffer & Delon, Mycotaxon 18: 166. 1983 = *Thielaviopsis neocaledoniae* Dadant, Rev. gén. Bot. 57: 176. 1950 [*nom. inval.*, Art. 36.1]

Description: Kiffer & Delon (1983, pp 166–170, Figs 1–2).

Phylogenetic data: Paulin-Mahady *et al.* (2002); Harrington (2009); Six *et al.* (2009); B. Wingfield *et al.* (2012).

Notes: Teleomorph unknown. This species groups in the *C. coerulescens* complex (Harrington 2009; B. Wingfield *et al.* 2012).

Ceratocystis norvegica J. Reid & Hausner, Botany 88: 977. 2010.

Anamorph: not observed.

Phylogenetic data: Reid *et al.* (2010).

Notes: This species is a member of the *C. coerulescens* species complex (Reid *et al.* 2010).

Ceratocystis oblonga R.N. Heath & Jol. Roux, Fungal Diversity 34: 59. 2009.

Anamorph: thielaviopsis-like.

Phylogenetic data: Heath *et al.* (2009); Tarigan *et al.* (2010); Kamgan Nkuekam *et al.* (2012b); Van Wyk *et al.* (2011b).

Notes: This species is a member of the *C. moniliformis* species complex (B. Wingfield *et al.* 2012).

Ceratocystis obpyriformis R.N. Heath & Jol. Roux, Fungal Diversity 34: 57. 2009.

Anamorph: thielaviopsis-like.

Phylogenetic data: Heath *et al.* (2009); Van Wyk *et al.* (2009a, 2011a, b); Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2011).

Notes: This species is a member of the *C. fimbriata* species complex (B. Wingfield *et al.* 2012).

Ceratocystis omanensis Al-Subhi, M.J. Wingf., M. van Wyk & Deadman, *In* Al-Subhi *et al.*, Mycol. Res. 110: 242. 2006.

Anamorph: thielaviopsis-like.

Phylogenetic data: Al-Subhi *et al.* (2006); Kamgan Nkuekam *et al.* (2008a, 2012b); Heath *et al.* (2009); Tarigan *et al.* (2010); Van Wyk *et al.* (2011b).

Notes: This species is a member of *Ceratocystis moniliformis* species complex (B. Wingfield *et al.* 2012).

Thielaviopsis ovoidea (Nag Raj & W.B. Kendr.) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 70. 2002 ≡ *Chalara ovoidea* Nag Raj & W.B. Kendr., *Monogr. Chalara p.* 127. 1975.

Description: Nag Raj & Kendrick (1975, pp 116, 127–128, Figs 43B).

Phylogenetic data: Paulin-Mahady *et al.* (2002); Heath *et al.* (2009); Six *et al.* (2009); B. Wingfield *et al.* 2012).

Notes: Teleomorph unknown. This species groups with *T. thielavioides* and *T. basicola* (Harrington 2009; B. Wingfield *et al.* 2012).

Ceratocystis papillata M. van Wyk & M.J. Wingf., Fungal Diveristy 40: 112. 2010.

Anamorph: thielaviopsis-like.

Phylogenetic data: Van Wyk *et al.* (2010, 2010, 2011a, b); Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2011).

Notes: This species is a member of the *C. fimbriata* species complex (B. Wingfield *et al.* 2012).

Ceratocystis paradoxa (Dade) C. Moreau, Rev. Mycol. (Paris) Suppl. Col.17: 22. 1952 ≡ *Sporoschisma paradoxum* De Seynes, Recherches pour Servir à l'Histoire Naturelle des Végétaux Inférieurs 3: 30. 1886 ≡ *Chalara paradoxa* (De Seynes) Sacc., Syll. Fung. 10: 595. 1892 ≡ *Thielaviopsis paradoxa* (De Seynes) Höhn., Hedwigia 43: 295. 1904 ≡ *Ceratostomella paradoxa* Dade, Trans. Br. Mycol. Soc. 13: 191. 1928 ≡ *Ophiostoma paradoxum* (Dade) Nannf., *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934 ≡ *Endoconidiophora paradoxa* (Dade) R.W. Davidson, J. Agric. Res. 50: 802. 1935 = *Thielaviopsis ethacetica* Went, Meded. Proefstn W. Java 'Kagok' 5: 4. 1893 [as *'ethaceticus'*] = *Endoconidium fragrans* Delacr., Bull. Soc. Mycol. Fr. 9: 184. 1893 = *Stilbochalara dimorpha* Ferd. & Winge, Bot. Tidsskr. 30: 220. 1910.

Anamorph: thielaviopsis-like.

Descriptions: Davidson (1935, pp 801–802); Hunt (1956, pp 13, 19–20); Morgan-Jones (1967c, Figs A-G); Nag Raj & Kendrick (1975, pp 112, 114, 128–129, Figs 41–42); Upadhyay (1981, p. 67, Figs 197–204).

Phylogenetic data: Hausner *et al.* (1993c); Witthuhn *et al.* (1999); Roux *et al.* (2000); Paulin-Mahady *et al.* (2002); Barnes *et al.* (2003a); Harrington (2009); Six *et al.* (2009); B. Wingfield *et al.* (2012).

Notes: Synonymies of *T. ethacetica*, *En. fragrans* and *St. dimorpha* with *C. paradoxa* were suggested by Nag Raj & Kendrick (1975) and Paulin-Mahady *et al.* (2002). *Ceratocystis paradoxa* groups outside the three major species complexes defined by B. Wingfield *et al.* (2012), forming the core of the *C. paradoxa* clade as defined by Harrington (2009). This is the type species of *Thielaviopsis*, and species in this clade will probably be classified in this genus in the future. The taxon apparently consists of several cryptic species in need of description (Harrington 2009).

Ceratocystis pinicola T.C. Harr. & M.J. Wingf., Can. J. Bot. 76: 1452. 1998.

Anamorph: thielaviopsis-like.

Description: Harrington & Wingfield (1998, pp 1452, 1454).

Phylogenetic data: Witthuhn *et al.* (1999, 2000); Loppnau & Breuil (2003); Harrington (2009); Six *et al.* (2009).

Notes: This is a member of *C. coerulescens* species complex (Harrington 2009; B. Wingfield *et al.* 2012). The name should not to be confused with *Leptographium pinicolum* or *Ophiostoma pinicola*.

Ceratocystis pirilliformis I. Barnes & M. J. Wingf., Mycologia 95: 867. 2003.

Anamorph: thielaviopsis-like.

Phylogenetic data: Barnes *et al.* (2003a); Roux *et al.* (2004); Van Wyk *et al.* (2004b, 2007a, b, 2009a, b, 2010, 2011a, b); Thorpe *et al.* (2005); Kamgan Nkuekam *et al.* (2008a, 2012b); Rodas *et al.* (2008); Heath *et al.* (2009); Kolařík & Hulcr (2009); Tarigan *et al.* (2011).

Notes: This is a cryptic species in the *C. fimbriata* species complex (B. Wingfield *et al.* 2012).

Ceratocystis platani (Walter) Engelbr. & T.C. Harr., Mycologia 97: 65. 2005 ≡ *Endoconidiophora fimbriata* f. *platani* Walter, Phytopathology 42: 236. 1952.

Anamorph: thielaviopsis-like.

Phylogenetic data: Baker *et al.* (2003); Engelbrecht & Harrington (2005); Van Wyk *et al.* (2007a, b, 2009a, b, 2010, 2011a, b); Rodas *et al.* (2008); Harrington (2009); Heath *et al.* (2009); Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2011).

Notes: This species was treated as the sycamore (*Platanus*) population of *C. fimbriata* in earlier studies (Santini & Capretti 2000; Barnes *et al.* 2001; Baker *et al.* 2003; Engelbrecht *et al.* 2004; Thorpe *et al.* 2005). It is a member of the *C. fimbriata* species complex (Harrington 2009; B. Wingfield *et al.* 2012).

Ceratocystis polonica (Siemaszko) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952. emend. T.C. Harr. & M.J. Wingf., Can. J. Bot. 76(8): 1452. 1998 [as *'polonicum'*] ≡ *Ophiostoma polonicum* Siemaszko, Planta Pol. 7: 32. 1939.

Anamorph: thielaviopsis-like (Marin *et al.* 2005).

Descriptions: Siemaszko (1939, pp 20, 32–33, Pl. IV Figs 1–10); Mathiesen (1951, pp 208–210); Hunt (1956, p. 27); Solheim (1986, pp 205–206); Yamaoka *et al.* (1997, pp 1217–1219); Harrington & Wingfield (1998, pp 1452–1453, 1455); Marin *et al.* (2005, pp 1142, 1144).

Phylogenetic data: Witthuhn *et al.* (1998, 1999, 2000); Loppnau & Breuil (2003); Marin *et al.* (2005); Harrington (2009); Heath *et al.* (2009); Six *et al.* (2009).

Notes: Siemaszko (1939) erroneously connected a leptographium-like anamorph to this species, leading Upadhyay (1981) to treat it as a synonym of *O. penicillatum.* Solheim (1986) and Harrington (1988) considered *C. polonica* distinct and Visser *et al.* (1995) confirmed its classification in *Ceratocystis* with DNA sequences. A neotype was designated by Harrington & Wingfield (1998). *Ceratocystis polonica* was distinguished from the morphologically similar *C. laricicola* by Witthuhn *et al.* (2000) and Harrington *et al.* (2002), based primarily on the different conifer host and bark beetle associate, and is considered part of the *C. coerulescens* species complex (Harrington 2009; B. Wingfield *et al.* 2012). Marin *et al.* (2009) showed that European and Japanese populations of *C. polonica* are genetically isolated and possibly in the process of speciation.

Ceratocystis polychroma M. van Wyk, M.J. Wingf. & E.C.Y. Liew, Stud. Mycol. 50, 278. 2004.

Anamorph: thielaviopsis-like.

Phylogenetic data: Van Wyk *et al.* (2004b, 2007a, b, 2009a, b, 2010, 2011a, b); Kamgan Nkuekam *et al.* (2008a, 2012b); Rodas *et al.* (2008); Heath *et al.* (2009).

Notes: This is a cryptic species in the *C. fimbriata* species complex (B. Wingfield *et al.* 2012).

Ceratocystis polyconidia R.N. Heath & Jol. Roux, Fungal Diversity 34: 53. 2009.

Anamorph: thielaviopsis-like.

Phylogenetic data: Heath *et al.* (2009); Van Wyk *et al.* (2009a, 2011a, b); Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2011).

Notes: This species is a member of the *C. fimbriata* species complex (B. Wingfield *et al.* 2012).

Thielaviopsis populi (Kiffer & Delon) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 70. 2002 = *Chalaropsis populi* Veldemann, Meded. Facult. Landb., Rijksunivers. Gent 36: 1001. 1971 [*nom. inval.*, Art. 36.1, 37.1] ≡ *Chalara populi* Veldemann *ex* Kiffer & Delon, Mycotaxon 18: 171. 1983.

Description: Kiffer & Delon (1983, pp 171–172, Figs 1–2).

Phylogenetic data: Paulin-Mahady *et al.* (2002); Harrington (2009); Heath *et al.* (2009); Six *et al.* (2009); B. Wingfield *et al.* (2012).

Notes: Teleomorph unknown. This species groups with *T. thielavioides* and *T. basicola* (Harrington 2009; B. Wingfield *et al.* 2012).

Ceratocystis radicicola (Bliss) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 ≡ *Ceratostomella radicicola* Bliss, Mycologia 33: 468. 1941 ≡ *Ophiostoma radicicolum* (Bliss) Arx, Antonie van Leeuwenhoek 18: 211. 1952 = *Chalaropsis punctulata* Hennebert, Antonie van Leeuwenhoek 33: 334. 1967 ≡ *Thielaviopsis punctulata* (Hennebert) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 70. 2001.

Anamorph: thielaviopsis-like.

Descriptions: Hunt (1956, pp 11, 17, 20); Nag Raj & Kendrick (1975, pp 106, 142, Fig. 38); Upadhyay (1981, p. 69, Figs 205–213).

Phylogenetic data: Hausner *et al.* (1993c); Witthuhn *et al.* (1999); Paulin-Mahady *et al.* (2002); B. Wingfield *et al.* (2012).

Notes: *Ceratocystis radicicola* groups outside of the three major species complexes defined in *Ceratocystis*, but peripherally to the *C. paradoxa* clade (Harrington 2009; B. Wingfield *et al.* 2012). Paulin-Mahady *et al.* (2002) confirmed the synonymy of *T. punctulata* and *C. radicicola* based on identical ITS sequences.

Ceratocystis resinifera T.C. Harr. & M.J. Wingf., Can. J. Bot. 76: 1449. 1998.

Anamorph: thielaviopsis-like.

Description: Harrington & Wingfield (1998, pp 1449, 1451–1452).

Phylogenetic data: Witthuhn *et al.* (2000); Barnes *et al.* (2003a); Loppnau & Breuil (2003); Harrington (2009); Heath *et al.* (2009); Six *et al.* (2009).

Notes: *Ceratocystis refinifera* is a member of *C. coerulescens* species complex (Harrington 2009; B. Wingfield *et al.* 2012).

Ceratocystis rufipenni M.J. Wingf., T.C. Harr. & H. Solheim, Can. J. Bot. 75: 828. 1997.

Anamorph: thielaviopsis-like.

Phylogenetic data: Witthuhn *et al.* (1998, 2000); Loppnau & Breuil (2003); Harrington (2009); Six *et al.* (2009).

Notes: This is a member of *C. coerulescens* species complex (Harrington 2009; B. Wingfield *et al.* 2012).

Ceratocystis savannae Kamgan & Jol. Roux, *In* Kamgan Nkuekam *et al.*, Fungal Diversity 29: 52. 2008.

Anamorph: thielaviopsis-like.

Phylogenetic data: Kamgan Nkuekam *et al.* (2008a, 2012b); Heath *et al.* (2009); Tarigan *et al.* (2010); Van Wyk *et al.* (2011b).

Notes: This species belongs to the *C. moniliformis* species complex (B. Wingfield *et al.* 2012).

Ceratocystis smalleyi J.A. Johnson & T.C. Harr., Mycologia 97: 1088. 2005.

Anamorph: thielaviopsis-like.

Phylogenetic data: Johnson *et al.* (2005); Van Wyk *et al.* (2007a, b, 2009a, b, 2010, 2011a, b); Rodas *et al.* (2008); Harrington (2009); Heath *et al.* (2009); Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2011).

Notes: This species is a member of the *C. fimbriata* species complex (Harrington 2009; B. Wingfield *et al.* 2012).

Ceratocystis sublaevis M. van Wyk & M.J. Wingf., Fungal Diversity 46: 128. 2011.

Anamorph: thielaviopsis-like.

Phylogenetic data: Van Wyk *et al.* (2011b).

Notes: This species is a member of the *C. moniliformis* species complex (Van Wyk *et al.* 2011b).

Ceratocystis sumatrana Tarigan, M. van Wyk & M.J. Wingf., Mycoscience 51: 60. 2010.

Anamorph: thielaviopsis-like.

Phylogenetic data: Tarigan *et al.* (2010).

Notes: This species is a member of the *C. moniliformis* species complex (Tarigan *et al.* 2010).

Ceratocystis tanganyicensis R.N. Heath & Jol. Roux, Fungal Diversity 34: 56. 2009.
Anamorph: thielaviopsis-like.
Phylogenetic data: Heath *et al.* (2009); Van Wyk *et al.* (2009a, 2010, 2011a, b); Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2011).
Notes: This species is a member of the *C. fimbriata* species complex (Tarigan *et al.* 2011).

Thielaviopsis thielavioides (Peyr.) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 70. 2002 ≡ *Chalaropsis thielavioides* Peyronel, Le Staz. sper. agric. 49: 58. 1916 ≡ *Chalara thielavioides* (Peyronel) Nag Raj & W.B. Kendr., *Monogr. Chalara p.* 136. 1975 = *Chalaropsis thielavioides* Peyr. var. *ramosissima* Sugiyama, J. Fac. Sci. Univ. Tokyo 10: 33. 1968.
Description: Nag Raj & Kendrick (1975, pp 117, 136–137, Fig. 44).
Phylogenetic data: Paulin-Mahady *et al.* (2002); Harrington (2009); Six *et al.* (2009); B. Wingfield *et al.* (2012).
Notes: Teleomorph unknown. *Thielaviopsis thielavioides* is the type species of *Chalaropsis* and belongs to a clade within *Ceratocystis s.l.* with species such as *T. basicola* (Paulin-Mahady *et al.* 2002; B. Wingfield *et al.* 2012).

Ceratocystis tribiliformis M. van Wyk & M.J. Wingf., *In* Van Wyk *et al.*, Fungal Diversity 21, 197. 2006.
Anamorph: thielaviopsis-like.
Phylogenetic data: Van Wyk *et al.* (2006a, 2011b); Kamgan Nkuekam *et al.* (2008a, 2012b); Heath *et al.* (2009); Tarigan *et al.* (2010).
Notes: *Ceratocystis tribiliformis* is a member of the *C. moniliformis* species complex (B. Wingfield *et al.* 2012).

Ambrosiella trypodendri (L.R. Batra) TC. Harr., *In* Harrington *et al.*, Mycotaxon 111: 355. 2010 ≡ *Phialophoropsis trypodendri* L.R. Batra, Mycologia 59: 1008. 1967.
Description: Batra (1967, pp 1008–1009, Figs 3, 24, 25).
Notes: Teleomorph unknown. *Ambrobiella trypodendri* is the type species of *Phialophoropsis* (Batra 1967). Although no cultures or material are available for this species, Harrington *et al.* (2010) argued that it is morphologically similar to *Ambrosiella* and provided a new combination for it. Seifert (unpublished) has also examined the type, which formed the basis for the drawing of this species in *The Genera of Hyphomycetes* (Seifert *et al*. 2011). Harrington *et al.* (2010) did not mention that their new combination implied that *Phialophoropsis* should be treated as synonym of *Ambrosiella*.

Ceratocystis tsitsikammensis Kamgan & Jol. Roux, *In* Kamgan Nkuekam *et al.*, Fungal Diversity 29: 50. 2008.
Anamorph: thielaviopsis-like.
Phylogenetic data: Kamgan Nkuekam *et al.* (2008a, 2012b); Heath *et al.* (2009); Van Wyk *et al.* (2009a, 2010, 2011a, b); Tarigan *et al.* (2011).
Notes: This species belongs to the *C. fimbriata* species complex (Tarigan *et al.* 2011).

Ceratocystis tyalla Kamgan & Jol. Roux, *In* Kamgan Nkuekam *et al.*, Antonie van Leeuwenhoek 101: 233. 2012.
Anamorph: thielaviopsis-like.
Phylogenetic data: Kamgan Nkuekam *et al.* (2012b).
Notes: This species is a member of the *C. moniliformis* species complex (Kamgan Nkuekam *et al.* 2012b).

Ceratocystis variospora (R.W. Davidson) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952. emend. J.A. Johnson & T.C. Harr., Mycologia 97: 1083. 2005 ≡ *Endoconidiophora variospora* R.W. Davidson, Mycologia 36: 303. 1944 ≡ *Ophiostoma variosporum* (R.W. Davidson) Arx, Antonie van Leeuwenhoek 18: 212. 1952 ≡ *Ceratocystis moniliformis* f. *variospora* C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 23. 1952 [*nom. inval*., Art. 36.1]

Anamorph: thielaviopsis-like.

Descriptions: Hunt (1956, pp 16–18); Johnson *et al.* (2005, pp 1082–1084, Figs 8–16).

Phylogenetic data: Johnson *et al.* (2005); Van Wyk *et al.* (2007a, b, 2009a, b, 2010, 2011a, b); Rodas *et al.* (2008); Harrington (2009); Heath *et al.* (2009); Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2011).

Notes: Moreau (1952) invalidly reduced *C. variospora* to a *formae* of *C. moniliformis.* Webster & Butler (1967), Upadhyay (1981), and Seifert *et al.* (1993) all treated *C. variospora* as synonym of *C. fimbriata*. Johnson *et al.* (2005) showed that it is a phylogenetically distinct species in the *C. fimbriata* complex (Harrington 2009; B. Wingfield *et al.* 2012).

Ceratocystis virescens (R.W. Davidson) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 ≡ *Endoconidiophora virescens* R.W. Davidson, Mycologia 36: 301. 1944 ≡ *Ophiostoma virescens* (R.W. Davidson) Arx, Antonie van Leeuwenhoek 18: 212. 1952.

Anamorph: thielaviopsis-like.

Description: Sameuls (1993, p. 16, Figs 1A–B).

Phylogenetic data: Witthuhn *et al.* (1998, 1999, 2000); Réblová & Winka (2000); Roux *et al.* (2000); Barnes *et al.* (2003a); Van Wyk *et al.* (2004a, b, 2007a, b, 2009a, b, 2010, 2011a, b); Al-Subhi *et al.* (2006); Kamgan Nkuekam *et al.* (2008a, 2012b); Rodas *et al.* (2008); Heath *et al.* (2009); Kolařík & Hulcr (2009); Six *et al.* (2009); Matsuda *et al.* (2010); Tarigan *et al.* (2010, 2011); Sakayaroj *et al.* (2011).

Notes: This species was considered a synonym of *C. coerulescens* by Hunt (1956), Olchowecki & Reid (1974), and Upadhyay (1981), but Nag Raj & Kendrick (1975), Gibbs (1993), Kile (1993), and Seifert *et al.* (1993), considered the two species distinct. The separation of the two species was confirmed by Witthuhn *et al.* (1998). Harrington *et al.* (1998), Witthuhn *et al.* (2000) and Harrington (2009) showed that *C. virescens* isolates separate into two groups based on phylogeny and host specificity, and these “should be recognized as distinct species” (Witthuhn *et al.* 2000). The two groups comprise a monophyletic lineage within the *C. coerulescens* complex (Witthuhn *et al.* 2000; Harrington 2009; B. Wingfield *et al.* 2012).

Ambrosiella xylebori Brader *ex* Arx & Hennebert, Mycopath. Mycol. Appl. 25: 314. 1965.

Descriptions: Brader (1964, pp 40–42); von Arx & Hennebert (1965, pp 312–315, Fig. 2); Batra (1967, pp 990–992, Figs 14–19).

Phylogenetic data: Cassar & Blackwell (1996); Rollins *et al.* (2001); Paulin-Mahady *et al.* (2002); Gebhardt *et al.* (2005); Harrington (2009); Massoumi Alamouti *et al.* (2009); Six *et al.* (2009); Matsuda *et al.* (2010).

Notes: Teleomorph unknown. This is the type species of *Ambrosiella.* The genus and species were invalidly described by Brader (1964) [Art. 37.1], but von Arx & Hennebert (1965) redescribed and validated both. *Ambrosiella xylebori* is part of a distinct lineage in *Ceratocystis s.l.* together with *A. hartigii* and *A. beaveri* (Harrington 2009, Massoumi Alamouti *et al.* 2009, Paulin-Mahady *et al.* 2002, Six *et al.* 2009).

Ceratocystis zombamontana R.N. Heath & Jol. Roux, Fungal Diversity 34: 53. 2009.

Anamorph: thielaviopsis-like.

Phylogenetic data: Heath *et al.* (2009); Van Wyk *et al.* (2009a, 2011a, b); Kamgan Nkuekam *et al.* (2012b); Tarigan *et al.* (2011).

Notes: This species is a member of the *C. fimbriata* species complex (Tarigan *et al.* 2011).

Cornuvesica Viljoen, M.J. Wingf. & Jacobs, Mycological Research 104: 366. 2000 [type species *Cor. falcata*]

Notes: The inclusion of this monotypic genus in the *Ceratocystidaceae* is discussed by De Beer *et al.* (2012).

Cornuvesica falcata (E.F. Wright & Cain) C.D. Viljoen, M.J. Wingf. & K. Jacobs, Mycol. Res. 104: 366. 2000 ≡ *Ceratocystis falcata* E.F. Wright & Cain, Can. J. Bot. 39: 1226. 1961 ≡ *Ceratocystiopsis falcata* (E.F. Wright & Cain) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 125. 1981.

Anamorph: thielaviopsis-like.

Descriptions: Olchowecki & Reid (1974, p. 1688); Rayner & Hudson (1977, pp 315–316, Fig. 1); Upadhyay (1981, p. 125, Figs 449–453); Hutchison & Reid (1988, pp 65–68); Hausner *et al.* (2003, pp 46–48).

Phylogenetic data: Hausner *et al.* (1993a, c, 2000); Hausner & Reid (2004); Hausner & Wang (2005).

Custingophora Stolk, Hennebert & Klopotek, Persoonia 5: 195. 1968 [type species *Cus. olivaceae*]

Note: *Custingophora* is presently known only from its anamorph. The anamorphs of *Knoxdaviesia* (= *Gondwanamyces*) were treated in *Custingophora* by Réblová & Winka (2000) and Kolařík & Hulcr (2009), but both Viljoen *et al.* (1999) and Van der Linde *et al.* (2012) considered *Custingophora* and *Knoxdaviesia* as separate genera. We consider *Custingophora* as distinct from *Knoxdaviesia* based on their phylogenetic distance, its much smaller conidia and the straight rather than sinuous conidiophores.

The anamorphs of *Chaetosphaeria aterrima* (Fuckel) Réblová (Réblová 1998) and *Cha. aspergilloides* M.E. Barr & J.L. Crane were referred to as unnamed *Custingophora* spp. *Cha. aterrima* was belongs to the *Hypocreales* (Réblová & Winka 2000). No sequence data exist for *Cha. aspergilloides*, but its anamorph has some substantial differences from *Cus. olivacea* (Barr & Crane 1979), suggesting that it is probably related to *Cha. aterrima* and not to *Custingophora.*

Custingophora olivaceae Stolk, Hennebert & Klopotek, *In* Stolk *&* Hennebert, Persoonia 5: 197. 1968.

Description: Stolk *&* Hennebert (1968, pp 197–199, Figs 3–4).

Phylogenetic data: Viljoen *et al.* (1999); Réblová & Winka (2000); Kolařík & Hulcr (2009); Van der Linde *et al.* (2012).

Graphium Corda, Icon. Fung. 1: 16. 1837. [type species *Graphium penicillioides*]
= *Rhexographium* M. Morelet, Ann. Soc. Sci. Nat. Arch. Toulon et du Var 47: 90. 1995. Anamorphic synonym. [type species *Rh. fimbriisporum*]

Teleomorphs unknown. Conidiomata macronematous, synnematous, determinate, with dematiaceous stipes. Hyphae of stipe pigmented, simple septate. Conidiophores penicillately branched, with two or three levels of branching, metulae often present. Conidiogenous cells in whorls of two to six, conidiogenesis enteroblastic, with percurrent, annelidic extension. Conidial mass a transparent, slimy droplet, darkening with age. Conidia hyaline, aseptate, cylindrical to obovoid, sometimes curved with age, bases truncate, often with distinct basal frill. In rare cases a synanamorph with monoblastic, obovoid, pigmented chlamydospore-like conidia is formed.

Note: The emended genus description is based on *G. penicillioides* and the seven other known species for which DNA sequence data are available (Cruywagen *et al.* 2010). We include only those species known to be classified with the *Graphiaceae* here; others are considered in an extended nomenclator of described *Graphium* species is List C1. Jacobs *et* *al.* (2003b) showed that *Rh. fimbriisporum* belongs in *Graphium* and we thus treat *Rhexographium* as a synonym.

The name of the fungal genus *Graphium* should not be confused with *Graphium* Scopoli, a genus of swallowtail butterflies (this chapter Table 1; De Beer *et al.* 2012).

Graphium adansoniae Cruywagen, Z.W. de Beer & Jol. Roux, Persoonia 25: 67. 2010.

Description and phylogenetic data: Cruywagen *et al.* (2010, p. 67, Figs 6a–d).

Graphium basitruncatum (Matsush.) Seifert & G. Okada, Stud. Mycol. 45: 184. 2000 ≡ *Stilbum basitruncatum* Matsush., *Microfungi of the Solomon Islands and Papua-New Guinea*: 62. 1971.

Description: Okada *et al.* (2000, p. 184, Figs 21, 24).

Phylogenetic data: Okada *et al.* (1998, 2000); Jacobs *et al.* (2003); Cruywagen *et al.* (2010); Paciura *et al.* (2010b); Lackner & de Hoog (2011).

Notes: This species was treated as synonym of *Gr. penicillioides* by Matsushima (1989), but Okada *et al.* (2000) showed that the species is distinct.

Graphium carbonarium Paciura, Z.W. de Beer, X.D. Zhou & M.J. Wingf., *In* Paciura *et al.*, Fungal Diversity 40: 85. 2010.

Description: Paciura *et al.* (2010b, p. 85, Figs 21–33).

Phylogenetic data: Paciura *et al.* (2010b); Cruywagen *et al.* (2010); Paciura *et al.* (2010b).

Graphium fabiforme Cruywagen, Z.W. de Beer & Jol. Roux, Persoonia 25: 69. 2010.

Description and phylogenetic data: Cruywagen *et al.* (2010, p. 69, Figs 6e-h).

Graphium fimbriisporum (M. Morelet) K. Jacobs, Kirisits & M.J. Wingf., Mycologia 95: 719. 2003 [as *'fimbriasporum'*] ≡ *Rhexographium fimbriisporum* M. Morelet, Ann. Soc. Sci. Nat. Arch. Toulon et du Var 47: 91. 1995 [as *'fimbriasporum'*]

Description: Jacobs *et al.* (2003, pp 719–721, Figs 1–7).

Phylogenetic data: Jacobs *et al.* (2003); Cruywagen *et al.* (2010); Paciura *et al.* (2010b); Lackner & de Hoog (2011).

Graphium laricis K. Jacobs, Kirisits & M.J. Wingf., Mycologia 95: 721. 2003.

Description: Jacobs *et al.* (2003, pp 721–724, Figs 10–22).

Phylogenetic data: Jacobs *et al.* (2003); Cruywagen *et al.* (2010); Paciura *et al.* (2010b); Lackner & de Hoog (2011).

Graphium madagascariense Cruywagen, Z.W. de Beer & Jol. Roux, Persoonia 25: 69. 2010.

Description and phylogenetic data: Cruywagen *et al.* (2010, p. 67, Figs 6i-l).

Graphium penicillioides Corda, Icon. Fung. 1: 18. 1837*.* emend. Okada & Seifert, *In* Okada *et al.*, Stud. Mycol. 45: 175. 2000.

Descriptions: Corda (1837, p. 18, Pl. 5 Fig. 25); Seifert & Okada (1993, pp 28–30, Figs 1A–B, 2); Okada *et al.* (2000, pp 175–177, Figs 3–20).

Phylogenetic data: Okada *et al.* (1998, 2000); Rainer *et al.* (2000); Jacobs *et al.* (2003); Cruywagen *et al.* (2010); Paciura *et al.* (2010b); Lackner & de Hoog (2011).

Notes: This is the type species of *Graphium*. An epitype was designated and the species delineated based on DNA sequences by Okada *et al.* (2000).

Graphium pseudormiticum M. Mouton & M.J. Wingf., *In* Mouton *et al.*, Mycol. Res. 98: 1273. 1994.

Descriptions: Mouton *et al.* (1994, 1273–1275, Figs 1–11); Paciura *et al.* (2010b, pp 84–85, Figs 19, 23, 27).

Phylogenetic data: Jacobs *et al.* (2003); Okada *et al.* (2000); Cruywagen *et al.* (2010); Paciura *et al.* (2010b); Lackner & de Hoog (2011).

Knoxdaviesia M.J. Wingf., P.S. van Wyk & Marasas, Mycologia 80: 26. 1988. emend. Z.W. de Beer, Seifert & M.J. Wingf [type species *K. proteae*]
= *Gondwanamyces* G.J. Marais & M.J. Wingf., *In* Marais *et al.*, Mycologia 90: 139. 1998. Teleomorphic synonym. [type species *Go. proteae*]

Perithecia black, globose; necks relatively long, cylindrical to slightly tapered toward the apex; ostiolar hyphae short or absent; asci evanescent; ascospores hyaline, aseptate, allantoid, with or without a lunate sheath. Conidiophores macronematous, mononematous, olivaceous-brown, septate, usually arising from rhizoids; stipe erect, unbranched, often sinuous on the upper part. Conidiogenous cells phialidic, produced in terminal whorls on each conidiophore, ovoid, with minute collarettes. Conidia hyaline, one-celled, smooth-walled, cylindrical to allantoid, rounded at the apex and truncate at the base, produced in mucoid masses at the apex of conidiophores.

Notes: The genus *Knoxdaviesia* was described for *K. proteae*, the anamorph of a species described at the same time as *Cop. proteae* (Wingfield *et al.* 1988). Marais *et al.* (1998) eventuallly proposed the teleomorph genus *Gondwanamyces* with *Go. proteae* as type species. Viljoen *et al.* (1999) showed that the anamorph genus *Custingophora* was closely related to *Gondwanamyces*, and Kolařík & Hulcr (2009) subsequently suggested that *Knoxdaviesia* and *Custingophora* should be treated as synonyms. This suggestion was rejected by Van der Linde *et al.* (2012). We concur with the separate treatment of these genera. Under the Melbourne Code the oldest name, *Knoxdaviesia*, has priority over *Gondwanamyces*. We thus redefine this genus to accommodate teleomorphic species and provide new combinations where needed.

Knoxdaviesia capensis M.J. Wingf. & P.S. van Wyk, Mycol. Res. 97: 710. 1993 ≡ *Custingophora capensis* (M.J. Wingf. & P.S. van Wyk) M. Kolařík, *In* Kolařík & Hulcr, Mycol. Res. 113: 58. 2009 = *Ophiostoma capense* M.J. Wingf. & P.S. van Wyk, Mycol. Res. 97: 710. 1993 ≡ *Gondwanamyces capensis* (M.J. Wingf. & P.S. van Wyk) G.J. Marais & M.J. Wingf., *In* Marais *et al.*, Mycologia 99: 140. 1998.

Descriptions: Wingfield & Van Wyk (1993, pp 710–713, Figs 1–19); Marais & Wingfield (2001, pp 243–246, Figs 20, 23).

Phylogenetic data: Marais *et al.* (1998); Viljoen *et al.* (1999); Wingfield *et al.* (1999); Harrington (2009); Kolařík & Hulcr (2009); Six *et al.* (2009); Van der Linde *et al.* (2012).

Knoxdaviesia cecropiae (M. Kolařík) Z.W. de Beer & M.J. Wingf. ***comb. nov.,*** **MB 801076** ≡ *Custingophora cecropiae* M. Kolařík, *In* Kolařík & Hulcr, Mycol. Res. 113: 50. 2009 (basionym) ≡ *Gondwanamyces cecropiae* (M. Kolařík) Van der Linde, Jol. Roux & M.J. Wingf., *In* Van der Linde *et al.*, Mycologia 104: 582. 2012.

Description: Kolařík & Hulcr (2009, p. 50, Figs 5, 6D-E).

Phylogenetic data: Kolařík & Hulcr (2009); Van der Linde *et al.* (2012).

Notes: Teleomorph unknown.

Knoxdaviesia proteae M.J. Wingf., P.S. van Wyk & Marasas, Mycologia 80: 26. 1988 ≡ *Custingophora proteae* (M.J. Wingf., P.S. van Wyk & Marasas) M. Kolařík, *In* Kolařík & Hulcr, Mycol. Res. 113: 58. 2009 = *Ceratocystiopsis proteae* M.J. Wingf., P.S. van Wyk & Marasas, Mycologia 80: 24. 1988 ≡ *Gondwanamyces proteae* (M.J. Wingf., P.S. van Wyk & Marasas) G.J. Marais & M.J. Wingf., *In* Marais *et al.*, Mycologia 90: 139. 1998.

Description: Wingfield *et al.* (1988, pp 24–27, Figs 1–15); Marais & Wingfield (2001, pp 243–246, Figs 19, 23).

Phylogenetic data: Hausner *et al.* (1993a, c, 2000); Marais *et al.* (1998); Viljoen *et al.* (1999); Wingfield *et al.* (1999); Réblová & Winka (2000); Gibb & Hausner (2003); Hausner &

Reid (2004); Hausner & Wang (2005); Kolařík & Hulcr (2009); Six *et al.* (2009); Van der Linde *et al.* (2012).

Knoxdaviesia scolytodis (M. Kolařík) Z.W. de Beer & M.J. Wingf. ***comb. nov.,*** **MB 801077** ≡ *Gondwanamyces scolytodis* M. Kolařík, *In* Kolařík & Hulcr, Mycol. Res. 113: 48. 2009 (basionym).

Description: Kolařík & Hulcr (2009, pp 50–56, Figs 4, 6A–C).

Phylogenetic data: Kolařík & Hulcr (2009); Van der Linde *et al.* (2012).

Notes: Teleomorph unknown.

Knoxdaviesia serotectus (Van der Linde & Jol. Roux) Z.W. de Beer & M.J. Wingf. ***comb. nov.,*** **MB 801078** ≡ *Gondwanamyces serotectus* Van der Linde & Jol. Roux, *In* Van der Linde *et al.*, Mycologia 104: 578. 2012 (basionym).

Description: Van der Linde *et al.* (2012, pp 578–579, Fig. 3).

Phylogenetic data: Van der Linde *et al.* (2012).

Notes: Teleomorph unknown.

Knoxdaviesia suidafrikana (Morgan-Jones & R.C. Sinclair) Z.W. de Beer & M.J. Wingf. ***comb. nov.,*** **MB 801079** ≡ *Custingophora suidafrikana* Morgan-Jones & R.C. Sinclair, Mycotaxon 11: 443. 1980 (basionym).

Description: Morgan-Jones & Sinclair (1980, pp 443–445, Fig. 1).

Notes: Teleomorph unknown. This species, originally described from decaying wood in South Africa (Morgan-Jones & Sinclair 1980), is morphologically very similar to the *K. undulatistipes* (Pinnoi *et al.* 2003), *K. serotectus* and *K. ubusi* (Van der Linde *et al.* 2012). It has conspicuously sinuous conidiophores, not present in *Cus. olivaceae*, and clearly belongs in *Knoxdaviesia*. However, the conidiophores of *K. suidafrikana* are almost double the length (230 µm) of those of *K. serotectus* and *K. ubusi*, and longer than those of all other species in the genus apart from *K. undulatistipes*.

Knoxdaviesia ubusi (Van der Linde & Jol. Roux) Z.W. de Beer & M.J. Wingf. ***comb. nov.,*** **MB 801080** ≡ *Gondwanamyces ubusi* Van der Linde & Jol. Roux, *In* Van der Linde *et al.*, Mycologia 104: 579. 2012 (basionym).

Description: Van der Linde *et al.* (2012, pp 579–582, Fig. 4).

Phylogenetic data: Van der Linde *et al.* (2012).

Notes: Teleomorph unknown.

Knoxdaviesia undulatistipes (Pinnoi) Z.W. de Beer & M.J. Wingf. ***comb. nov.,*** **MB 801081** ≡ *Custingophora undulatistipes* Pinnoi, *In* Pinnoi *et al.*, Nova Hedwigia 77: 214. 2003 (basionym).

Description: Pinnoi *et al.* (2003, pp 214–217, Figs 1–5).

Notes: Teleomorph unknown. This species, described from the petiole of a dead palm leaf in Thailand (Pinnoi *et al.* 2003), resembles *K. suidafrikana* (Morgan-Jones & Sinclair 1980), *K. serotectus* and *K. ubusi* (Van der Linde *et al.* 2012). In particular, the pronounced sinuation on the stipes that confirms its treatment in *Knoxdaviesia* rather than *Custingophora*. The conidiophores are the longest (210–520 µm) in the genus.

Knoxdaviesia wingfieldii (Roets & Dreyer), Z.W. de Beer & M.J. Wingf. ***comb. nov.*****, MB PENDING** ≡ *Gondwanamyces wingfieldii* Roets & Dreyer, *In* Crous *et al*., Persoonia 28: 138-182. 2012.

Description: Crous *et al.* (2012, pp 144-145).

Phylogenetic data: Crous *et al.* (2012).

Sphaeronaemella P. Karst., Hedwigia 23: 17. 1884 [type species *Sph. helvellae*]
= *Viennotidia* Negru & Verona *ex* Rogerson, Mycologia 62: 899. 1970. Teleomorphic synonym. [type species *Vi. spermosphaerici*] = *Viennotidia* Negru & Verona, Mycopath. Mycol. Appl. 30: 306. 1966 [*nom. inval*., Art. 37.1] = *Viennotidia* P.F. Cannon & D. Hawksw., Bot. J. Linn. Soc. 84: 155. 1982 [as '*Viennotidea'*] [type species *Vi. fimicola*] [superfluous validation]
= *Gabarnaudia* Samson & W. Gams, Stud. Mycol. 6: 88. 1974. Anamorphic synonym. [type species *Ga. betae*]
= *Ceratocystis* Ellis & Halst. section *Ophiostoma* (Syd.) H.P. Upadhyay *pro parte*, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 85. 1981.

Note: The uncertain placement of *Sphaeronaemella* in the *Microascales* is discussed by De Beer *et al.* (2012). Malloch (1974) and Cannon & Hawskworth (1982) recognized four, and Hausner & Reid (2004) five species of *Sphaeronaemella*. We list those five species below, and include *S. horanszkyi*, described in 1975, because there is reportedly material available for this species. However, 22 additional *Sphaeronaemella* spp. described prior to 1950 are listed in Index Fungorum (www.indexfungorum.org/) and are not considered further here; they should be considered in future treatments of the genus. Malloch (1974) suggested the synonymy of *Viennotidia* with *Sphaeronaemella*, supported by Hutchison & Reid (1988a) and then confirmedusing molecular data by Hausner *&* Reid (2004). Hausner & Reid (2004) and De Beer *et al.* (2012) showed that *G. betae* groups within *Sphaeronaemella*, rendering *Gabarnaudia* a synonym of *Sphaeronaemella* under the Melbourne Code. Upadhyay (1981) designated formal sections in *Ceratocystis*. Although most of the taxa he included in his section *Ophiostoma* are now included in *Ophiostoma s.l.*, he also treated *S. helvellae* and *S. fimicola* in this section.

Sphaeronaemella betae (Delacr.) Z.W. de Beer & M.J. Wingf. ***comb. nov.,*** **MB 801093** ≡ *Oospora betae* Delacr., Bull. Soc. mycol. Fr. 13: 116. 1897 (basionym) ≡ *Penicillium betae* (Delacr.) Biourge, La Cellule 33: 100. 1923 ≡ *Paecilomyces betae* (Delacr.) Cornford, Trans. Br. Mycol. Soc. 43: 155. 1960 ≡ *Gabarnaudia betae* (Delacr.) Samson & W. Gams, *In* Samson, Stud. Mycol. 6: 90. 1974 = *Oospora lasiosphaeriae* G. Arnaud, Bull. Trimest. Soc. mycol. Fr. 68: 195 (1952) [*nom. inval*., Art. 36.1]

Descriptions: Samson (1974, pp 90–93, Figs 358a–b, 39a–c); Matsushima (1993, No. 875, Figs 552–554).

Phylogenetic data: Hausner & Reid (2004); De Beer *et al.* (2012).

Note: *Gabarnaudia betae* is the type species of *Gabarnaudia* (Samson 1974), and groups in a well-supported monophyletic clade with *S. helvellae*, the type species of *Sphaeronaemella*. Although no teleomorph has been observed for this species, *Ga. betae* is thus transferred to *Sphaeronaemella.* Samson (1974) listed *O. lasiosphaeriae* as synonym of *Ga. betae*.

Sphaeronaemella fimicola Marchal, Bull. Soc. Roy. Bot. Belg. 30: 143. 1891 ≡ *Gabarnaudia fimicola* Samson & W. Gams., *In* Samson, Stud. Mycol. 6: 92. 1974 ≡ *Ceratocystis fimicola* (Marchal) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 95. 1981 ≡ *Viennotidia fimicola* (Marchal) P.F. Cannon & D. Hawksw., Bot. J. Linn. Soc. 84: 157. 1982 [as '*Viennotidea*'] = *Sphaeronaemella fimicola var. minor* Marchal, Bull. Soc. Roy. Bot. Belg. 30: 143. 1891.

Anamorph: gabarnaudia-like.

Descriptions: Saccardo (1892, p. 407); Grove (1937, p. 115); Samson (1974, pp 92–94, Fig. 40); Upadhyay (1981, p. 95, Figs 344–347); Hutchison & Reid (1988a, pp 76, 78–79).

Phylogenetic data: Hausner *et al.* (1993c, 2000); González *et al.* (2000); Hausner & Reid (2004); Hausner & Wang (2005); Kolařík & Hulcr (2009); De Beer *et al.* (2012).

Sphaeronaemella helvellae (P. Karst.) P. Karst., Hedwigia 23: 18. 1884 ≡ *Sphaeria helvellae* P. Karst., Fungi Fenn. Exs. no. 674. 1867 ≡ *Sphaeronaema helvellae* (P. Karst.) Jacz., Nouv. Mem. Soc. Imp. Nat. Moscow, 15: 302. 1898 ≡ *Ceratocystis helvellae* (P. Karst.) H.P. Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis,* p. 97. 1981 = *Melanospora karstenii* Arx & E. Müll., Beitr. Kryptogamenflora Schweiz 11: 1.46. 1954.

Anamorph: not observed (Samson 1974).

Descriptions: Saccardo (1886, p. 618); Upadhyay (1981, p. 97, Figs 348–352); Malloch (1974, pp 1–2, Figs 1–7).

Phylogenetic data: Hausner & Reid (2004); Hausner & Wang (2005); De Beer *et al.* (2012).

Sphaeronaemella horanszkyi (Tóth) Tóth, Ann. Hist.-Nat. Mus. Hung. 67: 33. 1975 ≡ *Ceratocystis horanszkyi* Tóth, Ann. Hist.-Nat. Mus. Hung. 55: 182. 1963 [as *'horánszkyi'*]

Anamorph: not observed.

Notes: We examined the holotype of this species (BP 36413, Department of Botany, Hungarian Natural History Museum, Budapest), and agree that it belongs in *Sphaeronaemella*. A note included with the holotype by the late J.C. Krug (Toronto, 1977) questions the distinction of this species from *S. fimicola*. We retain the species as distinct until further study can resolve this possible synonymy.

Sphaeronaemella humicola Samson & W. Gams, *In* Samson, Stud. Mycol. 6: 94. 1974 ≡ *Gabarnaudia humicola* Samson & W. Gams, *In* Samson, Stud. Mycol. 6: 94. 1974 ≡ *Viennotidia humicola* (Samson & Gams) P.F. Cannon & D. Hawksw., J. Linn. Soc., Bot. 84(2): 158. 1982 [as *'Viennotidea'*]

Anamorph: gabarnaudia-like.

Description: Samson *et al.* (1974, pp 94–96, Fig. 41, Pl. 2).

Notes: This species differs from other *Sphaeronaemella* spp. because the ascomata do not produce necks or ostioles, and it has ellipsoidal rather than allantoid or orange-section shaped ascospores. *Sphaeronaemella humicola* was not included in *Ceratocystis* with *S. helvellae* and *S. fimicola* by Upadhyay (1981). The ex-type culture (CBS 115.72) no longer represents the correct fungus (Hausner & Reid 2004), and its placement in *Sphaeronaemella* needs reconsideration.

Sphaeronaemella raphani Malloch, Fungi Canadenses 53. 1974 ≡ *Viennotidia raphani* Negru & Verona, Mycopath. Mycol. Appl. 30: 307. 1966 [*nom. inval*., Art. 37.1] ≡ *Viennotidia raphani* (Malloch) P.F. Cannon & D. Hawksw., Bot. J. Linn. Soc. 84: 158. 1982 [as *'Viennotidea'*]

Anamorph: not observed.

Notes: Upadhyay (1981) considered this a *nomen dubium.* Cannon & Hawksworth (1982) reported that there was no type material but transferred the species to *Viennotidia* because they believed the fungus could be recognized from the protologue.

Sphaeronaemella spermosphaerici (Negru & Verona) Malloch, Fungi Canadenses no. 53. 1974 ≡ *Viennotidia spermosphaerici* Negru & Verona, Mycopath. Mycol. Appl. 30: 306. 1966 [*nom. inval*., Art. 37.1] ≡ *Viennotidia spermosphaerici* Negru & Verona *ex* Rogerson, Mycologia 62: 899. 1970 ≡ *Viennotidia spermosphaerici* P.F. Cannon & D. Hawksw., Bot. J. Linn. Soc. 84: 159. 1982 [as *'Viennotidea'*] [superfluous validation]

Anamorph: not observed.

Notes: Cannon & Hawksworth (1982) reported that there was no type material but transferred the species to *Viennotidia* because they believed the fungus could be recognized from the protologue.

B.2. VALID SPECIES OF UNCERTAIN STATUS (*MICROASCALES*)

Ceratocystis autographa Bakshi, Ann. Bot. n.s. 15: 55. 1951.

Synanamorphs: thielaviopsis- and sporothrix-like*.*

Descriptions: Bakshi (1951, pp 55–60, Pl. VI Figs 4–7); Hunt (1956, pp 11, 13, 23); Olchowecki & Reid (1974, p. 1695); Nag Raj & Kendrick (1975, pp 86, 140–141 Fig. 28C); Upadhyay (1981, p. 73, Figs 223–231); Wingfield *et al.* (1995, pp 1290, 1292, Figs 1–10).

Phylogenetic data: Hausner *et al.* (1993c).

Notes: *Ceratocystis autographa* groups distantly from *Ophiostoma* and *Ceratocystis* according to Hausner *et al.* (1993c), who suggested, “the disposition of this species must await the availability of strains from fresh teleomorph material.” We agree that the generic placement of this species requires careful consideration in light of its two unlikely synanamorphs*.* Wingfield *et al.* (1995) and Coetzee *et al.* (2000) also treated it as a doubtful species.

Gabarnaudia cucumeris (Peck) de Hoog & W. Gams, *In* de Hoog *et al.*, Stud. Mycol. 29: 103. 1986 ≡ *Oospora cucumeris* Peck, Ann. Rep. N.Y. St. Mus. 41: 80. 1888 ≡ *Alysidium cucumeris* (Peck) Pound & Clem., *In* Pound *et al.*, Minn. Bot. Stud. 9: 650. 1896.

Description: Saccardo (1892, p. 513).

Notes: De Hoog *et al.* (1986) transferred this species to *Gabarnaudia* based on the original desciption, but also remarked, “we therefore do not doubt that Peck’s fungus is identical to *G. betae*…’. In view of the cryptic descriptions for this species, we consider the status of this species uncertain.

Gabarnaudia tholispora Samson & W. Gams, *In* Samson, Stud. Mycol. 6: 96. 1974 ≡ *Oospora tholispora* G. Arnaud, Bull. Trimest. Soc. Mycol. Fr. 68: 195. 1952 [*nom. inval.*, Art. 36.1]

Description: Samson (1974, pp 96–97, Figs 38c–e, 39e–f).

Notes: The morphology of this species differs somewhat from that of other *Sphaeronaemella* spp. (Samson 1974). We thus prefer not to include it in the genus without DNA sequence data.

B.4. INVALIDLY PUBLISHED SPECIES (*MICROASCALES*)

Ceratocystis antennaroidospora Roldan, Philip. J. Sci. 91: 415–423. 1962 [*nom. inval*., Art. 37.1]

Anamorph: thielaviopsis-like.

Notes: Although Nag Raj & Kendrick (1975) considered this name illegitimate because the species was described as a species of *Ceratocystis* when no teleomorph structures were present, such an interpretation was only relevant for a brief period of time in the progressive versions of the ICBN. With the advent of the Melbourne Code it would be possible to validate the name by neotypification (Art. 9.6) if this fungus was rediscovered.

Ceratocystis asteroides Roldan, Philip. J. Sci. 91: 421. 1962 [*nom. inval.*, Art. 37.1]

Synanamorphs: thielaviopsis-like and synnematal (Roldan 1962).

Notes: This combination of synanamorphs is atypical for *Ceratocystis* species and maty indicate that the name was based on a mixed culture. Otherwise, the situation for this species is identical to that noted for *C. antennaroidospora* (see above).

Ceratocystis heveae G.H. Zhao, J. Nanjing Forestry University 16: 82. 1992 [*nom. inval*., Art. 37.5]

Anamorph: thielaviopsis-like.

Notes: Although a Latin description was supplied and microscope slides were deposited at Nanjing Forestry University (NFU-WAH), the material was not assigned numbers or explicitly indicated as the holotype. The species is thus invalidly published (Art. 37.5). To validate the species, a lectotype should be designated (Art. 9.2), and this is most appropriately done by someone who can examine the original material.

Ceratocystis jezoensis Aoshima, Ph.D. thesis, University of Tokyo: 9. 1965 [*nom. inval.*, Art. 29.1 & 36.1]

Anamorph: thielaviopsis-like.

Notes: This species was invalidly described, isolated from both *Ips typographus* f. *japonicus* infesting spruce, and *Ips subelongatus* (as *I. cembrae*) infesting larch in Japan (Aoshima 1965). The collection of isolates of Aoshima probably represented two morphologically similar, but host-specific species, *C. polonica* and *C. fujiensis* (Yamaoka *et al.* 1997, 1998; Marin *et al.* 2005).

Ceratocystis pidoplichikovii Milko, Izv. Mold. Fil. Akad. Nauk SSSR 4(82): 61. 1961 [*nom. inval.*, Art. 37.1] [as *'pidoplichikovi'*]

Anamorph: thielaviopsis-like.

Description: Potlajczuk & Schekunova (1985, p. 150).

Notes: According to the original description, the ascomata and ascospores resemble those of *Cop. minuta*, while the anamorph is clearly thielaviopsis-like, with phialidic conidiogenesis, also producing chlamydospores.

Thielaviopsis wallemiiformis Dominik & Ihnat., Zesz. nauk. wyzsz. Szk. roln. Szczec. 50: 24. 1975 [as *'wallemiaeformis'*] [*nom. invalid*., 37.1]

Notes: Kiffer & Delon (1983) first pointed out the problems with the typification of this species, named for the appearance of its chlamydospores, which mimic *Wallemia*. If necessary, the name could be validated by accurate typificaiton.

C. SPECIES EXCLUDED FROM THE OPHIOSTOMATOID GENERA IN THE *OPHIOSTOMATALES* AND *MICROASCALES*

C.1. SPECIES DESCRIBED IN THE CLASSICAL CONCEPT OF *GRAPHIUM*

As noted by Okada *et al.* (1998, 2000) and discussed further in the accompanying paper by De Beer & Wingfield (2012), the historical concept of *Graphium* has evolved in the 180 years since its description. Conceptual revisions were offered by Saccardo (1886), Hedgcock (1906), Goidànich (1935b), Crane & Schocknecht (1973), before the genus was conclusively removed from the group we now call the *Ophiostomatales* (Okada *et al.* (2000). The accepted species of *Graphium sensu stricto* in the *Microascales* are listed above. Most other species are considered here, largely based on type studies undertaken during monographic revision of *Stilbella* (Seifert 1985), though most of it not published in that work.

As noted elsewhere in this volume by De Beer *et* al. (2012), the classical concept of *Graphium* included all darkly pigmented synnematous fungus, and thus included species with dry, aseptate conidia that would now be classified in genera such as *Cephalotrichum, Phaeoisaria, Nodulisporium* or *Dematophora* (the latter two now likely to be subsumed under their respective teleomorphs in *Hypoxylon* or *Rosellinia*), or cercosporoid genera of the *Capnodiales* with phragmoconidia, such as *Phaeoisariopsis, Phacellium,* or *Graphiothecium*. Species with slimy ameroconidia occur in several groups, and Seifert & Okada (1993) and Okada *et al.* (2000) found that such species with percurrent conidiogenous cells occurred in several different lineages, including *Exophiala* (*Eurotiomycetes*), *Graphium* and now *Parascedosporium* (Lackner & de Hoog 2011), the latter two representing distinct lineages in the *Microascales*. Similar fungi with conidia produced from phialides can be distributed among *Stilbocrea*, *Crinula*, *Dendrostilbella* and other genera.

Graphium adustum Grosmann, Z. Parasitenk. 3: 95. 1931.

Notes: This species is reported as a common associate of *Dryocoetes autographus* on *Picea excelsa .* The protologue is very brief and includes no illustration. As with *Gr. pycnocephalum,* noted below, the initially hyaline synnemata and subglobose conidia do not suggest either a member of the *Ophiostomatales* or of *Graphium s.str.* We were unsuccessful at finding a type in ZT.

Graphium aeruginosum (Desm.) Sacc., Syll. fung. 4: 618. 1886 ≡ *Stilbum aeruginosum* Desm., Annls Sci. nat., Bot. 19: 434. 1830 : Fr., Syst. mycol. 3: 303. 1832 ≡ *Ceratopodium aeruginosum* (Desm.) Kuntze, Rev. Gen. Pl. 2: 847. 1891.

Notes: Seifert (1985) could not fully characterize the fragmented synnematous fungus on the holotype (PC) and considered the species a *nomen dubium*. However, photographs of a recent collection from Mexico, unfortunately not saved, on the Mushroom Observer web site (mushroomobserver.org/94326?q=N8Y3) are consistent with our observations of the type, indicating the species will eventually be recollected, can be epitypified, and its taxonomy reconsidered.

Graphium ailanthi (Ranoj. & Bubák) Sacc., Syll. fung. 22: 1448. 1913 ≡ *Dendrostilbella ailanthi* Ranoj. & Bubák, Annls mycol. 8: 401. 1910.

Notes: Seifert (1985) did not locate a type in B, nor is it recorded in the BPI database. A culture isolated from the same host genus by C.T. Rogerson (75-235) is a species of *Parascedosporium*.

Graphium albiziae (Pat.) Pat., *In* Duss, Enum. Champ. Guadeloupe (Lons-le-Saunier): 93 (1903 ≡ *Isaria albiziae* Pat., Bull. Soc. mycol. Fr. 16: 187. 1900.

Notes: The holotype is in S (F40431), but we have not had an opportunity to examine it. We have not seen the original diagnosis and cannot comment on the possible identity of this fungus.

Graphium albonigrescens Lindau, Rabenhorst Krypt. Fl., Pilze 9: 362. 1910.

Notes: Lindau created this superfluous name for *Graphium leucocephalum* (Berk. & Curt.) Sacc. [non *G. leucocephalum* (Wallr.) Sacc.]. Saccardo had earlier proposed the new name *G. Curtisii* Sacc. to replace the Berkeley & Curtis epithet. As noted by Seifert (1985, as *Stilbella*), the fungus is facultative synonym of *Stilbocrea aterrima* (see below).

Graphium album (Corda) Sacc., Syll. fung. 4: 618. 1886 ≡ *Ceratopodium album* Corda, Icon. Fung. 1: 19. 1837.

Notes: No authentic material of this fungus is in the Corda herbarium in PR. The original description of black synnemata with a white capitulum, and the illustration by Corda, give no clue to its identity.The species description for *G. album* was emended by Hedgcock (1906), an act that has no nomenclatural significance. An isolate identified by Mathiesen-Käärik as *G. album* (CBS 276.54 = JCM 9744 = C 1225) and treated as such by Okada *et al.* (2000) and Jacobs *et al.* (2003), was shown by Harrington *et al.* (2001) to be identical to the ex-type isolate of *P. erubescens* (CBS 278.54 = JCM 9747 = C1222), now treated as anamorph of *G. cucullata*. The actual identity of *G. album* remains unknown, and unless authentic material is eventually discovered, there is no point in considering this name any further.

Graphium altissimum Strasser, Verh. zool.-bot. Ges. Wien 73: 233. 1924 ("1923").

Notes: Authentic material (W14904, W15060) is very similar to *Stilbocrea atterima* (see above). Conidia are slightly smaller, and the ornamenting cells on the synnema stipe are less distinct, indicating that this might represent a different species. Neither specimen conforms to the collecting dates noted in the protologue, but we refrain from lectotypifying the species pending searches in other herbaria. There are no cultures or DNA sequences for *Gr. atterima*, thus this synonymy can be tentatively proposed for now.

Graphium ambrosiigerum Hedgc., Mo. Bot. Gard. Rep. 17: 88. 1906.

Notes: This species was included by Goidànich (1935b) in his broader concept of *Graphium* that included ophiostomatalean species with sporothrix-like anamorphs. Harrington *et al.* (2001) suggested that it did not belong in the *Ophiostomatales*, but found the type material (BPI) to be in such poor condition that they could not conclusively place it in *Graphium s. str.* or any other genus.

Graphium angamosense Matsush., Mycol. Mem. 8: 21. 1995.

Notes: The protologue of this species has good illustrations showing light brown, almost hyaline synnemata with elongated conidia with basal frills.The conidiogenous cells are not clearly visible, making it difficult to decide whether this species belongs to *Graphium s.str*. or the *Ophiostomatales*, but the former seems quite likely to KAS. The type material will have to be investigated to confirm its generic placement.

Graphium anomalum (Berk.) Sacc., Syll. fung. 4: 618. 1886 ≡ *Stilbum anomalum* Berk., Mag. Zool. Bot. 1: 49. 1837 ≡ *Ceratopodium anomalum* (Berk.) Kuntze, Rev. Gen. Pl. 2: 847. 1891.

Notes: There is no properly labelled type in K. There is a specimen labelled with the unpublished name "*Isaria anomala* B. & Br.", with an annotation "*Stilbum*" in the *Graphium* folder in K, which could represent the type, but the habitat appears to be dung instead of the plant material suggested in the protologue. The illustration in the protologue is perhaps more suggestive of a myxostelid. There seems to be little point in considering this name further.

Graphium anomalum Massee, Kew Bulletin 1908: 218. *nom. illegit.* Art. 53 [non *G. anomalum* (Berk.) Sacc. 1886] .

Notes: The type specimen (K) is an anamorphic *Poronia* sp. (*Xylariales*), which would have been classified in the genus *Lindquistia* Subram. & Chandrash. under dual nomenclature (Seifert *et al.* 2011). Because the name is illegitimate, there is no reason to reintroduce it as a *Poronia* species.

Graphium aphthosae Alstrup & D. Hawksw., Meddr Grønland, Biosc. 31: 37. 1990.

Notes: This species is associated with lichens and produces its conidia in chains (Alstrup & Hawksworth 1990). Neither character corresponds with species of *Graphium s.str.* Otherwise, the species is similar to *Gr. samogiticum* (see below). We exclude it from *Graphium s.str.* and the *Ophiostomatales,* and the species will have to be reevaluated to determine its appropriate classification.

Graphium aspergilloides Speg., Michelia 1: 476. 1879 = *Sporocybe aspergilloides* (Speg.) Sacc., Syll. fung. 4: 608. 1886 ≡ *Cephalotrichum aspergilloides* (Speg.) Kuntze, Rev. Gen. Pl. 3: 453. 1898 (as *aspergillodes*) ≡ *Papilionospora aspergilloides* (Speg.) Rao & Sutton, Kavaka 3: 23. 1973.

Notes: The type is not in LPS or PAD, as noted by Rao & Sutton (1973). This is the type species of *Papilionospora*, which produces peculiar butterfly-like conidia resulting from the anastomosis of adjacent ameroconidia originating on adjacent denticles on sympodial conidiogenous cells. Its phylogenetic affinities are unknown. Rao & Sutton (1973) did not address typification conclusively. No illustration accompanies the protologue of *Gr. aspergilloides*, and because there are no authentic specimens, there are no known supplementary illustrations of the type Spegazzini often drew on herbarium packets. Thus, we designate the material studied by Rao & Sutton (1973), the specimen IMI 177253, as the **neotype** for *Gr. aspergilloides*, and thus as the neotype of the genus *Papilionospora*.

Graphium aterrimum (Welw. & Curr.) Sacc., Syll. fung. 4: 611. 1886 ≡ *Stilbum aterrimum* Welw. & Curr., Trans. Linn. Soc. London 26: 291. 1870 (basionym) ≡ *Stilbella aterrima* (Welw. & Curr.) Seifert, Stud. mycol. 27: 91. 1985 ≡ *Gracilistilbella aterrima* (Welw. & Curr.) Seifert, Stud. mycol. 45: 18. 2000 ≡ *Stilbocrea aterrima* (Welw. & Curr.) Seifert, **comb. nov. MB 801094**.

Notes: Because *Stilbocrea*, formerly considered a teleomorph genus, predates *Gracilistilbella* Seifert 2000, this anamorphic species is transferred here to this genus in the

Bionectriaceae, Hypocreales. The species is described and illustrated by Seifert (1985); see further notes below under *Gr. clavulatum*.

Graphium atrovirens Hedgc., Mo. Bot. Gard. Rep. 17: 88. 1906.

Notes: According to Hedgcock (1906), this species bears its conidia in a typical slimy head, has a sporothrix-like synanamorphs. It seems likely to be a member of *Ophiostoma s.l.* It was included in *Graphium* by Goidànich (1935b), who treated all pesotum-like anamorphs of *Ophiostoma s.l.* in this genus. Hedgcock distributed exsiccati to several herbaria, mostly dried cultures on wood wafers that appear to have been prepared in an overheated oven; they are usually almost impossible to interpret morphologically (Seifert, unpubl.).The holotype (BPI 448682) and other specimens from Hedgcock are available and careful study should be undertaken to determine if generic placement is possible.

Graphium atrum Desm., Ann. Sci. Nat., 111, 10: 343. 1848 ≡ *Sporocybe atra* (Desm.) Sacc., Syll. fung. 4: 608. 1886 [non *S. atrum* (Corda) Fr., 1849] ≡ *Phaeostilbella atra* (Desm.) Höhn., Mitt. Bot. Techn. Hochsch. Wien, 2: 72. 1925 ≡ *Saccardaea atra* (Desm.) E.W. Mason & M.B. Ellis, Mycol. Pap. 56: 40. 1953 ≡ *Myrothecium atrum* (Desm.) M.C. Tulloch, Mycol. Pap. 130: 31. 1972.

Notes: Seifert (1985) and Seifert *et al.* (2011) considered this species correctly classified in *Phaeostilbella*. See below under *Gr. nigrum.*

Graphium bambusae **(**Höhn.) Sacc., Syll. fung. 22: 1448. 1913 ≡ *Phaeoisaria bambusae* Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 118: 329. 1909.

Notes: This is a synonym of *Phaeoisaria clematidis,* according to de Hoog & Papendorf (1976), who examined the holotype (FH). We examined an isotype (K), which lacked diagnostic characters.

Graphium berkeleyi Mont., Annls Sci. Nat., Bot., sér. 4 8: 303. 1857 ≡ *Stysanus berkeleyi* (Mont.) Sacc., Syll. fung. 4: 623. 1886 ≡ *Coremium berkeleyi* (Mont.) Pound & Clem., Minn. bot. Stud. 1, Bull. 9: 728. 1897.

Notes: The holotype is not in K or UPS, and was not examined by Morton & Smith (1963). The description of a dark, branched synnematous fungus with catenate, fusoid conidia 15 x 5 µm, growing on the pileus of an unidentified polypore may be explicit enough to allow this fungus to be recognized if recollected. It is unlikely to be either a true *Graphium* or a member of the *Ophiostomatales*.

Graphium bicolor (Pers.) Sacc., Syll. fung. 4: 618. 1886 ≡ *Stilbum bicolor* Pers., Syn. fung. p. 682. 1801 = *Ceratopodium cavipes* (Oud.) Kuntze, Rev. Gen. Pl. 2: 847. 1891.

Notes: There is no specimen of *Stilbum bicolor* in Persoon's herbarium (L). Seifert (1985) noted that the name had been applied to a variety of synnematous fungi with bicoloured synnemata. The uncertainly about its correct application suggests that the name should be rejected.

Graphium bolivarii Riofrio, Mem. Soc. exp. Hist. nat. 15: 388. 1929.

Notes: We have not located the type of this fungus, described as producing yellow synnemata on rotten stems of tomato. The description is reminiscent of the synnematous anamorphs of *Sphaerostilbella* spp., or possibly *Volutella citronella* (Cooke & Massee) Seifert.

Graphium bulbicola Henn., Hedwigia 44: 177. 1905.

Notes: The holotype (S) is a member of the *Parascedosporium putredinus* complex, but the name was not considered by Lackner & de Hoog (2011). Its delimitation or synonymy should be considered in future studies of the complex.

Graphium caliciiforme Maire, Bull. trimest. Soc. mycol. Fr. 46: 243. 1930.
Notes: The description and illustration suggest that this may be a synonym of *Phaeostilbella nigra* (see below under *Gr. nigra*). We have not seen the type.

Graphium calicioides (Fr.) Cooke & Massee, *In* Cooke, Grevillea 16 (no. 77): 11. 1887 ≡ *Sporocybe calicioides* Fr., Syst. mycol. 3: 343. 1832 ≡ *Calicium haustellare* Ach., K. Vetensk-Acad. Nya Handl., p. 122. 1816.
Notes: Okada *et al.* (2000) treated this species as *Exophiala calicioides* (Fr.) G. Okada & Seifert (*Chaetothyriales*), after examining slides of the holotype of *C. haustellare* in DAOM. The species and its taxonomic history are discussed extensively by Mason & Ellis (1953), and much more succinctly by Ellis (1971, both as *Graphium*). See notes under *Gr. flexuosum* and *Gr. rigidum* below.

Graphium cartwrightii J.F.H. Beyma, Antonie van Leeuwenhoek 6: 281. 1939.
Notes: Mason & Ellis (1953) considered this a synonym of *Pachnocybe ferruginea* Berk., (*Pachnocybales*, *Pucciniomycetes*), which makes synnema-like basidiomata, and explained the circumstances that lead van Beyma to describe this species in *Graphium.* The ex-type culture is CBS 123.41. The synonymy is now generally accepted.

Graphium cavipes (Oudem.) Sacc., Syll. fung. 4: 619. 1886 ≡ *Stilbum cavipes* Oudem., Hedwigia 22: 62. 1883 ≡ *Ceratopodium cavipes* (Oudem.) Kuntze, Rev. Gen. Pl. 2: 847. 1886.
Notes: The type is not in the Oudemans herbarium in L. The description and published illustration, which features a submerged globose base, and coprophilous habit, suggest the fungus is identical with *Sphaeronaemella fimicola* Marchal.

Graphium ceratostomoides Speg., An. Soc. Cient. Argent. 10: 165. 1880 ≡ *Ceratopodium ceratostomoides* (Speg.) Kuntze, Rev. Gen. Plt. 2: 847. 1891 ≡ *Graphiopsis ceratostomoides* (Speg.) Goid., Annali Bot., Roma 21: 9, 1935.
Notes: The holotype (LPS 33.133), contains no synnemata, but the drawing on the packet suggests a species of *Phaeoisaria*. De Hoog and Papendorf (1976), also examined the type, and considered Spegazzini's species a synonym of *Phaeoisaria clematidis* (Fuckel) Hughes.

Graphium chlorocephalum (Speg.) Sacc., Syll. fung. 4: 613. 1886 ≡ *Sporocybe chlorocephala* Speg., An. Soc. Cient. Arg. 13: 31. 1882.
Notes: Based on study of the holotype (LPS 33.141), this is a facultative synonym of *Stromatographium stromaticum* (Berk.) Höhnel (Seifert 1987).

Graphium cicadicola Speg., Anal. Mus. nac. B. Aires, Ser. 3 13: 446. 1910.
Notes: The type specimen (LPS 12.273) is *Purpureocillium lilacinus* (Thom) Luangsa-ard, Houbraken, Hywel-Jones & Samson, as was also examined by Samson (1974), who first proposed the synonymy (as *Paecilomyces*).

Graphium cinerellum Speg., *In* Thumen, Pilze Weinstockes p. 55. 1878 = *Ceratopodium cinerellum* (Speg.) Kuntze, Rev. Gen. Pl. 2: 847. 1891.
Notes: A specimen and a drawing are available from Spegazzini's herbarium. We here designate the drawing (LPS 33.134) as the lectotype for *Gr. cinerellum*; it suggests *Cephalotrichum microsporum* (Sacc.) P.M. Kirk. The herbarium material (LPS 12.270) contains only broken synnemata with no conidiogenous cells or conidia.

Graphium clavaeforme Preuss, Linnaeae 24: 133. 1851 = *Stilbum clavaeforme* (Preuss) Goid., Annali Bot., Roma 21: 49. 1935 = *Ceratopodium clavaeforme* (Preuss) Kuntze, Rev. Gen. Pl. 2: 847. 1891.

Notes: The holotype is not in B (Seifert 1985). The protologue does not contain enough detail to meaningfully neotypify this name, which should probably be considered for rejection.

Graphium clavisporum Berk. & Cooke, Grevilla 3: 100. 1874 = *Isariopsis clavispora* (Berk. & Cooke) Sacc., Sylloge 4: 631. 1886.

Notes: The type specimen (K, Car. Inf. #1813) confirms that this is a synonym of *Pseudocercospora vitis* (Lév.) Speg., as suggested by Jong & Morris (1970).

Graphium clavula (Berk. & Broome) Sacc., Syll. fung. 4: 617. 1886 ≡ *Stilbum clavula* Berk & Broome, J. Linn. Soc., Bot. 14: 97. 1875 = *Ceratopodium clavular* (Berk. & Broome) Kuntze, Rev. Gen. Pl. 2: 847. 1891.

Notes: Seifert (1985) was unable to completely characterize this fungus from the holotype (K, *Graphium* folder 2909). It is not a true *Graphium*, nor a member of the *Ophiostomatales*, but is possibly an anamorph of the *Xylariales,* such as those represented by the name *Acanthodochium* Samuels, J.D. Rogers & Nagas.

Graphium clavulatum (Mont.) Sacc., Syll. fung. 4: 617. 1886 ≡ *Stilbum clavulatum* Mont., Ann. Sci. Nat. Bot. Dec. V, VI, VII, et VIII. 18: 248. 1842 ≡ *Graphiopsis clavulata* (Mont.) Goid., Annali Bot., Roma 21: 48. 1935 ≡ *Stilbella clavulata* (Mont.) Seifert, Stud. mycol. 27: 85. 1985 ≡ *Gracilistilbella clavulata* (Mont.) Seifert, Stud. Mycol. 45: 18. 2000.

Notes: In dual name nomenclature, this was the oldest epithet available for the anamorph of *Stilbocrea gracilipes* (Tul. & Tul.) Samuels & Seifert. The latter represents both the oldest genus name and species epithet, and now is the correct name for the species. This species, and the very similar *Stilbocrea atterima*, are both common in subtropical and tropical areas and produce dark synnemata with slimy conidial heads, and were often confused with the classical concept of *Graphium*. The conidiogenous cells are obviously phialidic, however, and the synnemata also feature conspicuously warty ornamenting cells (Seifert 1985).

Graphium coffeae Zimm., Zentbl. Bakt. ParasitKde, Abt. II, 7: 145. 1901.

Notes: The holotype is not in B or BO. We have not seen the original publication, which included an illustration, and cannot comment on the possible identity of this fungus.

Graphium comatrichoides Massee & Salmon, Ann. Bot. 16: 88, 1902.

Notes: No type or authentic material could be located in K. The habitat on dung and the drawing published with the protologue are consistent with the present concept of *Parascedosporium putredinis* (Corda) M. Lackner & de Hoog, although no conidiogenous cells are figured. We designate Figs. 89–91 in the protologue as the lectotype for this name.

Graphium coralloides (Berk. & M.A. Curtis) Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 118: 894. 1909 ≡ *Cordierites coralloides* Berk. & M.A. Curtis, *In* Berkeley, J. Linn. Soc., Bot. 10: 370 1869 ('1868').

Notes: Rifai (1968) clarified the confusion that led to the transfer of *C. coralloides* to *Graphium*. The discomycete referred to by this name is not the same fungus as the anamorph observed by Höhnel (1909), and thus this epithet cannot be applied to that anamorph. *Dennisographium ustulinae* (Pat.) Seifert is the appropriate name for this anamorph, and although *Gr. coralloides sensu* Höhnel is the same fungus, it is not technically a synonym.

Graphium coryneoides (Ellis & Everh.) Sacc., Syll. fung. 4: 617. 1886 ≡ *Stilbum coryneoides* Ellis & Everh., J. Mycol. 1: 1 53. 1885 ≡ *Ceratopodium coryneoides* (Ellis & Everh.) Kuntze, Rev. Gen. Pl. 2: 847. 1891.

Notes: A facultative synonym of *Stilbocrea gracilipes* (Tul. & Tul.) Samuels & Seifert. according to Seifert (1985, as *Stilbella*). See additional notes under *Gr. clavulatum* above.

Graphium cuneiferum (Berk. & Broome) E.W. Mason & M.B. Ellis, Mycol. Pap. 56: 41. 1953 ≡ *Stilbum cuneiferum* Berk. & Broome, Ann. Mag. nat. Hist., ser. 14, 15: 33. 1875 ≡ *Sporocybe cuneifera* (Berk. & Broome) Sacc., Syll. fung. 4: 606. 1886 ≡ *Cephalotrichum cuneiferum* (Berk. & Broome) Kuntze, Rev. Gen. Pl. 3: 453. 1898.

Notes: Seifert (1985) examined the holotype (K) and considered this a synonym of the fungus now known as *Parascedosporium putredinis* (Corda) M. Lackner & de Hoog (Lackner & de Hoog 2011). However, the type also has scattered perithecia of what may be a species of *Petriella*; if this is the teleomorph, then the synonymy should be reconsidered.

Graphium curtisii Sacc., Syll. Fung. 4: 808. 1886.

Notes: This new name was proposed by Saccardo for *Gr. leucocephalum* (Berk. & Curt.) Sacc. when he realized that he had also created the name *G. leucocephalum* (Wallr.) Sacc., 1886 in the same publication. It is a synonym of *Stilbocrea atterima* (see above).

Graphium curvulum Berk. & Br., J. Linn. Soc. Bot. 14: 100. 1875 = *Arthrobotryum curvulum* (Berk. & Br.) Sacc., Syll. fung. 4: 629. 1886.

Notes: Petch (1924) located the type of this fungus (Thwaites 342) under the name *Thelephora pedicellata* in K*,* where it was still filed when KAS visited in 1983. There are no synnemata on the type. The protologue describes 6–7 septate conidia; we observed one pigmented, rostrate, 6-distoseptate conidium, 27 x 5.5 µm. Clearly this is not a species of *Graphium s. str.* or of *Ophiostoma s.l.* and it should be reconsidered, if necessary, in any future revisions of *Arthrobotryum* Ces.

Graphium cylindricum Petch. Ann. R. Bot. Gard. Peraden. 9: 329, 1925.

Notes: The holotype in K is a synnematous *Nodulisporium* sp. Many described species of *Graphium* are synnematous anamorphs of the *Xylariaceae*, which would until recently have been described in *Nodulisporium* Preuss or *Dematophora* Hartig. Modern species concepts in this family have been derived mostly from teleomorphic characters, and it is generally impossible to correlate these anamorphs with known species of *Hypoxylon, Rosellinia* or other teleomorph-defined genera in the family. For this reason, new combinations are not proposed and it is left for future taxonomists studying this family whether any of these anamorph names should be retained.

Graphium desmazieri Sacc., Syll. fung.1: 254. 1882 ≡ *Pleurographium desmazieri* (Sacc.) Goid., Annali Bot., Roma 21: 48. 1935.

Notes: Described as the anamorph of *Rosellinia desmazierri* (Berk. & Broome) Sacc., this species was destributed in Saccardo's Mycotheca Venata under number 1574; copies in BR and K are a species of *Dematophora* Hartig. The name was apparently never transferred to *Dematophora,* the genus used for synnematous anamorphs of *Rosellinia*. See notes under *Gr. cylindricum.*

Graphium dubautiae F. Stevens & Weedon, Bull. Bernice P. Bishop Mus 19: 159. 1925.

Notes: The holotype (ILL 16378) matches the illustration in the protologue, and represents a fasciculate cercosporoid fungus reminiscent of *Phacellium* and similar genera. It is neither a true *Graphium* nor a member of the *Ophiostomatales.*

Graphium dulcamarae (Sacc.) Lindau, Rabenh. Krypt. Flora, 2 Aufl., I (Pilze), 9: 364. 1908 ≡ *Graphium fissum* Preuss var. *dulcamarae* Sacc., Syll. fung. 4: 610. 1886.

Notes: Hughes (1958) considered this a synonym of *Phaeoisaria clematidis*.

Graphium eumorphum (Sacc.) Sacc., Syll. fung. 4: 611. 1886 ≡ *Sporocybe eumorphum* Sacc., *Fungi italici autographice delineati,* no. 942. 1881 (diagnosis: Michelia 2: 560. 1882).

Notes: Although the catalogue of Saccardo’s herbarium (Gola 1930) indicates that the type of *Sporocybe eumorphum* exists, we did not receive it when requested in 1983. The protologue includes a drawing generally similar to *Parascedosporium putredinis*, although conidiogenous cells are not shown. Hedgcock (1906) identified some collections from wood in the USA as this species, and described a synanamorph that could either represent the sporothrix-like synanamorph of a species of *Ophiostoma s.l.*, or the mononematous, sympodial synanamorphs originally represented by the name *Parascedosporium*. No mention was made of a synanamorph in the original descriptions (Saccardo 1882, 1886), and we doubt that Hedgcock's specimens actually represented the same species. Frágner & Hejzlar (1973) identified strains causing human disease with this name and deposited an isolate as CBS 987.73 (=JCM 9753). This was included as a representative for the species by Okada *et al.* (2000), who showed it grouped in the '*G. putredinis* aggregate', and Lackner & de Hoog (2011) noted that the isolate had an identical ITS sequence to the ex-type isolate of *Pseudallescheria apiosperma*. This true identitity of *G. eumorphum sensu* Saccardo can only be ascertained if the holotype is relocated and re-examined.

Graphium explicatum Berk. & M.A. Curtis, Grevillea 3: 101. 1875.
Notes: The unpublished drawing accompanying the authentic specimens in K suggests a synnematous *Nodulisporium* sp. See notes under *Gr. cylindricum*.

Graphium fasciculatum Sacc., Michelia 1: 76. 1877 ≡ *Harpographium fasciculatum* (Sacc.) Sacc., Michelia 2: 33. 1880.
Notes: This species is well accepted as the type of *Harpographium* Sacc. (Seifert *et al*. 2011).

Graphium filifilense Sacc., Atti Mem. R. Accad. Sci., Lett., Arti, Padova 33: 194. 1917 ≡ *Graphiopsis filfilense* (Sacc.) Goid., Annali Bot., Roma 21: 48, 1935.
Notes: The holotype (PAD) is not a species of *Graphium,* and is possibly a species of the synnematous hyphomycete genus *Paathramaya* Subram.

Graphium fissum Preuss, Flora, Jena 34, no. 113. 1851 (see also Linnaea 24: 133. 1851) ≡ *Graphiopsis fissa* (Preuss) Bainier, Bull. Soc. mycol. Fr. 23: 19. 1907.
Notes: De Hoog & Papendorf (1976) examined the holotype (B), and observed percurrent conidiogenous cells and mucoid conidial masses, without providing additional details. An identification with *Graphium s. str.* or the anamorph of a member of the *Ophiostomatales* is at least possible. See also *Gr. dulcamarae* above.

Graphium flavovirens (Alb. & Schw.) Sacc., Syll. fung. 4: 618. 1886 ≡ *Periconia flavovirens* Alb. & Schw., Consp. fung. Lusat. p. 357. 1857 ≡ *Cephalotrichum flavovirens* (Alb. & Schw.) Nees, Syst. p. 87. 1817 ≡ *Stilbum flavovirens* (Alb. & Schw.) Link, Willd., Sp. pl., ed. 4, 6(2): 111. 1825 ≡ *Ceratopodium flavovirens* (Alb. & Schw.) Corda, Icon. Fung. 1: 19. 1837.
Notes: The holotype is not in PH or BPI. Seifert (1985) considered this a *nomen dubium*. The illustration with the protologue is suggestive of a species of *Cephalotrichum* Link, but the name was not considered in the only modern revision of this genus (Morton & Smith 1963, as *Doratomyces*).

Graphium flexuosum (Massee) Sacc., Syll. fung. 4: 611. 1886 ≡ *Stilbum flexuosum* Massee, J. Roy. Microscop. Soc. 5: 758. 1885 ≡ *Ceratopodium flexuosum* (Massee) Kuntze, Rev. Gen. Pl. 2: 847. 1891 ≡ *Sporocybe flexuosa* (Massee) E.W. Mason, Annotated Acct of Fungi rec'd I.M.I. 2, Fasc. 3: 127. 1941.
Notes: The holotype could not be located in Massee's herbaria in K (Mason & Ellis 1953) or NY (Seifert 1985). Mason & Ellis (1953) examined several specimens identified with this name collected in Great Britain by contemporaries of Massee, and considered them identical with *Exophiala calicioides* (Fr.) G. Okada & Seifert (as *Graphium*). The synonymy was tentatively accepted by Hughes (1958).

Graphium fructicola Marchal & É.J. Marchal, Bull. Acad. R. Sci. Belg., Cl. Sci. 4: 26. 1921.

Notes: We were unsuccessful at finding authentic material during a visit to BR in 1983, nor is the type in Gembloux. An SSU sequence of an isolate identified with this name (CBS 107.68 = JCM 9748, not authentic) labelled as *Gr. fructicola* groups within the *Parascedosporium putredinis* complex (Okada *et al.* 2000). Lackner & de Hoog (2011) did not include this isolate in their study, but suggested that it might represent a species of *Pseudallescheria.*

Graphium fuegianum Speg., Bol. Acad. Nac. Cienc. Cordoba 11: 307. 1888.

Notes: The type specimen (LPS 33.135) contains only sterile dematiaceous fascicles of hyphae. Höhnel believed it could be the same as *Stromatographium stromaticum* (Berk.) Höhnel (1909), but this seem unlikely because of the conspicuous, waxy stroma produced by the latter species (Seifert 1987).

Graphium geranii Voglino, Annals R. Accad. Agric. Torin 47: 412. 1904 ≡ *Graphiopsis geranii* (Voglino) Goid., Annali Bot., Roma 21: 48. 1935 ≡ *Phacellium geranii* (Voglino) U. Braun, Nova Hedwigia 56: 437. 1993.

Notes: The holotype (PAD) contains no structures matching the protologue, although necrotic leaf spots are present as described. The illustration with the protologue is consistent with the current classification of this species in the synnematous genus *Phacellium* Bonord.

Graphium giganteum (Peck) Sacc., Syll. fung. 4: 611. 1886 [*nom. illegit.* Art. 53.1, non Speg. 1886] ≡ *Stilbum giganteum* Peck, Rep. N.Y. St. Mus. 24: 93. 1872 ≡ *Graphium magnum* Sacc. & P. Syd., Syll. fung. 14: 1111. 1899 ≡ *Ceratopodium giganteum* (Peck) Kuntze, Rev. Gen. Pl. 2: 847. 1891.

Notes: Seifert (1985) examined the holotype (NYS) and considered this species a synonym of *Crinula caliciiformis* Fr. Because it was published in the same year as Spegazzini's fungus (below), *Gr. magnum* was introduced as a new name for Peck's in *Graphium,* although the original description in *Stilbum* was legitimate.

Graphium giganteum Speg., Anal. Soc. cient. argent. 22: 219. 1886.

Notes: The type specimen (LPS 15.262) is a synnematous species of *Nodulisporium*. See notes under *Gr. cylindricum.*

Graphium glaucocephalum (Corda) Sacc., Syll. fung. 4: 616. 1886 ≡ *Periconia glaucocephala* Corda, Icon. fung. 3: 13. 1839 ≡ *Sporocybe glaucocephala* Bonord., Handb. allgem. Mykol. p. 138. 1851.

Notes: The holotype is not in Corda's herbaria in PRM or K. The illustration with the protologue is clearly a synnematous fungus. This, and the occurrence of the species on stems of *Urtica* is suggestive of a member of the *Parascedosporium putredinis* complex. If a member of this complex is shown to have a preference for this substrate, it may be appropriate to take up this name.

Graphium glaucum Preuss, Linnaea 24: 133. 1851.

Notes: The holotype was not received when requested from B in 1984, although it is listed in the catalogue of Preuss's herbarium (Jülich 1974). The protologue is too vague to allow this fungus to be recognized without examination of the type, if still extant.

Graphium gordoniae Sawada, Special Publication College of Agriculture, National Taiwan University 8: 233. 1959 [*nom. inval.*, Art. 36.1]

Notes: We have not examined the type. The protologue describes, but does not illustrate, a synnematous fungus causing leaf spots on *Gordonia axillaris* in Taiwan. This species clearly does not belong to *Graphium s.str.* or *Ophiostoma s.l.* Validation and reclassification of the name would be an option if a synnematous fungus causing the same symptoms were to be recollected.

Graphium gracile Peck, Ann. Rep. N.Y. St. Mus. nat. Hist. 34: 50. 1883 ("1881").
Notes: The holotype (NYS!), on leaves of *Rubus strigosus,* is probably a species of *Phacellium*. None of the species accepted in the monograph by Braun (1998) are reported from *Rubus*. The species should be reconsidered in future revisions of *Phacellium.*

Graphium graminum Cooke & Massee, Grevillea 16: 11. 1887.
Notes: As mentioned previously by Morton and Smith (1963), our examination of the type of *G. graminum* (K) confirms the synonym of this name with *Cephalotrichum microsporum* (Sacc.) P.M. Kirk.

Graphium griseum (Berk.) Sacc., Syll. fung. 4: 616. 1886 ≡ *Pachnocybe grisea* Berk., *In* Smith's English Flora, vol. 5 pt. II: 34. 1836 ≡ *Sporocybe grisea* (Berk.) Goid., Annali Bot., Roma 21: 49. 1935.
Notes: The holotype in Berkeley's herbarium (K, King's Cliff, May 1841) is identical with *Cephalotrichum purpureofuscum* (Schw.) S. Hughes*,* as stated by Morton & Smith (1963).

Graphium grovei Sacc., Syll. fung. 4: 613. 1886 ≡ *Pachnocybe clavulata* Grove, J. Bot., London 23: 168. 1885 ≡ *Phaeoisaria clavulata* (Grove) E.W. Mason & S. Hughes, Mycol. Pap. 56: 42.1953.
Notes: Saccardo renamed Grove's species when he transferred it to *Graphium*, because the epithet *clavulatum* was already occupied by *Graphium clavulatum* (Mont.) Sacc. Mason & Hughes (in Mason & Ellis 1953) transferred Grove's species to *Phaeoisaria*, where it is now known as *P. clavulata*. The holotype (K) is in very poor condition, but probably represents the fungus now known as *P. clavulata*

Graphium guttuliferum Pidopl., Fungus Flora on Coarse Fodders, p. 57. 1948. (in Russian, p. 303, 1953 in English).
Notes: We have not seen the holotype. The species was described from common millet, *Panicum miliaceum*, with graphium-like synnemata and oblong conidia 4–10.5 x 2–3 µm.

Graphium hamamelidis J.M. Hook, Proc. Indiana Acad. Sci 1925: 231. 1926 ≡ *Stilbella hamamelidis* (J.M. Hook) Overholts, Mycologia 35: 253. 1943.
Notes: The type was not examined by Seifert (1985), but it seems likely that this is a synonym of *Gonatobotryum apiculatum* (Peck) S. Hughes.

Graphium hendersonulae Chevaug., Encycl. Mycol. 28: 87. 1956.
Notes: We have not seen specimens or the original publication of this species, and cannot comment on its possible identity.

Graphium hippotrichoides (Lindau) Sacc., Syll. fung. 22: 1449. 1913 ≡ *Clavularia hippotrichoides* Lindau, Rabenh. Krypt. Fl. Ed. 2, 1(9) 313. 1910 ≡ *Tilachlidiopsis hippotrichoides* (Lindau) Keissl., Annln naturh. Mus. Wien 37: 216. 1924 ≡ *Nematographium hippotrichoides* (Lindau) Goid., Annali Bot., Roma 21: 46. 1935.
Notes: Gams *et al*. (2010) lectotypified the entomogenous hyphomycete genus *Nematographium* Goid. with this species, after examining the holotype (B).

Graphium indicum Chouhan & Panwar, Indian Phytopath. 33: 289. 1980.
Notes: The type specimen, IMI 187995, is the fungus renamed above as *Stilbocrea atterima*, as noted by Seifert (1985, as *Stilbella*).

Graphium irradians Petr., Sydowia 4: 577. 1950.
Notes: We have not seen the holotype. Petrak's detailed description does not refer to a mucoid or liquid conidial mass, which would exclude the species from *Graphium s.str.*

Graphium klebahnii Oud., Arch. néerl. Sci., Sér. 2, 7: 295. 1902.

Notes: No material could be found in Oudeman's herbarium (L). The illustration, with its setose capitulum, is suggestive of the synnematous anamorph *Ophiostoma setosum,* but the illustrated allantoid conidia do not match. There does not seem to be any reason to further consider this name, and we recommend that it be placed on the 'rejected list' for the *Microascales.*

Graphium laxum Ellis, Bull. Torrey Bot. Club 8: 65. 1881 ≡ *Isariopsis laxa* (Ellis) Sacc., Syll. fung. 4: 631. 1886 ≡ *Phaeoisariopsis laxum* (Ellis) Jong & Morris, Mycopath. Mycol. appl. 34: 269. 1968.

Notes: Ellis (1971) considered this is a synonym of *Phaeoisariopsis griseola* (Sacc.) Ferraris, now known as *Pseudocercospora griseola* (Sacc.) Crous & U. Braun. Our examination of the type specimen of *G. laxum* in NY (Harris no. 1363) corroborates this conclusion.

Graphium leguminum Cooke, Grevillea 16: 71. 1888.

Notes: The holotype of this species (K) on *Rhynchosia tomentosa* is similar to *Phacellium carneum* (Oud.) U. Braun as described by Braun (1998), which grows on *Lathyrus pratensis,* a member of the same host family. It should be considered in future revisions of that genus.

Graphium lesnei (Vuill.) Castell. & Chalm., *Manual of tropical medicine*, p. 1121. 1919 ≡ *Rhinocladium lesnei* Vuill., Bull. Séanc. Soc. Sci. Nancy, Sér. 3, 11: 143. 1910.

Notes: This species was shown to be a synonym of *Parascedosporium putredinis* (Corda) M. Lackner & de Hoog, based on morphological examination and ITS sequencing of the ex-type strain, CBS 108.10 (Lackner & de Hoog 2011).

Graphium leucocephalum (Wallr.) Sacc., Syll. fung. 4: 615. 1886 [non *Graphium leucocephalum* (Berk. & Curt.) Sacc., 1886] ≡ *Cephalotrichum leucocephalum* Wallr., Fl. crypt. Germ. 2: 330. 1833.

Notes: Morton & Smith (1963) considered this a synonym of *Cephalotrichum purpureofuscum* (Schw.) S. Hughes, although Wallroth's type has apparently not been re-examined by a modern author.

Graphium leucocephalum (Berk. & Curt.) Sacc, Syll. fung. 4 : 611. 1886 [non *Gr. leucocephalum* (Wallr.) Sacc. 1886] ≡ *Stilbum leucocephalum* Berk. & Curt., Grevillea 3: 64. 1874.

Notes: The holotype in K (and an isotype in NY) demonstrate the synonymy of this species with *Stilbocrea atterima* (Seifert 1985). See notes under *Gr. curtisii* and *Gr. clavulatum* above.

Graphium leucophaeum Penzig & Sacc., Malpighia 15: 253. 1901 ≡ *Nematographium leucophaeum* (Penzig & Sacc.) Goid., Annali Bot., Roma 21: 46. 1935.

Notes: The holotype (BO 3486) contains only decapitated synnemata, but the few conidia seen and the presence of collapsed ornamenting cells on the stipes suggest that this is a synonym of *Stilbocrea gracilipes* (see above under *Gr. clavulata*).

Graphium ligulariae Săvul. & Sandu, Hedwigia 75: 229. 1935 ≡ *Phacellium ligulariae* (Săvul. & Sandu) U. Braun, Nova Hedwigia 56: 437. 1993.

Notes: The holotype (BUCM 36807) was examined by Braun (1993) and the reclassification in *Phacellium* is accepted here. An isotype is deposited as BPI 448760.

Graphium linderae Ellis & Everh., J. Mycol. 1: 4. 1885 ≡ *Isariopsis linderae* (Ellis & Everh.) Sacc., Syll. fung. 4: 631. 1886 ≡ *Exosporium linderae* (Ellis & Everh.) Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 125: 117. 1916 ≡ *Helminthosporium linderae* (Ellis &

Everh.) Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 125: 117. 1916 ≡ *Phaeoisariopsis linderae* (Ellis & Everh.) S.C. Jong & E.F. Morris, Mycopath. Mycol. appl. 34: 269. 1968 ≡ *Bitunicostilbe linderae* (Ellis & Everh.) M. Morelet, Bull. Soc. Sci. nat. Arch. Toulon et du Var 195: 7. 1971.

Notes: Our observations of the holotype (NY), and of supplementary authentic material (North American Fungi no. 1384) are consistent with the description by Jong & Morris (1968). The species is clearly not a member of *Graphium* or a member of the *Ophiostomatales*, and should probably be classified in *Spiropes* Cif.

Graphium macrocarpum Corda, Icon. Fung. 3: 13. 1839 ≡ *Harpographium macrocarpum* (Corda) Sacc., Syll. fung. 4: 620. 1886 ≡ *Sterigmatobotrys macrocarpa* (Corda) S. Hughes, Can. J. Bot. 36: 814. 1958.

Notes: This is the currently used name for the type species of *Sterigmatobotrys* Oudem. The holotype (PRM 155517) and the epitype added to extend the species and generic concept to include a teleomorph (PRM 915682), were included in the description by Réblová & Seifert (2011).

Graphium magnum Sacc. & P. Syd., Syll. fung. 14: 1111. 1899 ≡ *Graphium giganteum* (Peck) Sacc., Syll. fung. 4: 611. 1886 [*nom. illegit.* Art. 53.1, non *Gr. giganteum* Speg. 1886]

Notes: See under *G. giganteum* above.

Graphium malorum Kidd & Beaumont, Trans. Br. mycol. Soc. 10: 113. 1924.

Notes: We have not seen the type of this fungus. The authors compared their fungus with *Gr. fructicola,* another dubious name. The synnemata are large, described as up to 1 cm tall. We are not aware of a graphium-like fungus on apples with synnemata of this size, and the identity of the species cannot be ascertained until the type, if extant, is located.

Graphium melanotes (Syd.) Sacc., Sylloge 22: 1449. 1913 ≡ *Stilbum melanotes* Syd., Hedwigia 49: 84. 1910.

Notes: Seifert (1985) examined Sydow’s type (S) and considered this a synonym of *Crinula byssogena* (Berk. & Broome) Seifert.

Graphium minutellum Pidopl., Fungus Flora on Coarse Fodders, p. 58. 1948 (in Russian, p. 303, 1953, in English).

Notes: We have not seen the holotype of this fungus, described as producing very short synnemata less than 25 µm long, and ellipsoidal conidia 5.5–6.5 x 3.5 µm. Its identity remains unknown.

Graphium nanum (Ehrenb.) Sacc., Syll. fung. 4: 616. 1886 ≡ *Periconia nana* Ehrenb., Sylv. mycol. berol. p. 24. 1818 ≡ *Stilbum nanum* (Ehrenb.) Spreng., Syst. veg. ed 16, 4 (1): 547. 1827 [non *S. nanum* Massee] ≡ *Cephalotrichum nanum* (Ehrenb.) S. Hughes, Can. J. Bot. 36: 744. 1958 ≡ *Doratomyces nanus* (Ehrenb.) F.J. Morton & G. Sm., Mycol. Pap. 86: 80. 1963.

Notes: Slides of authentic material (DAOM 48495, 49382) prepared by Hughes (1958) confirm that the species is properly classified in *Cephalotrichum*. Ehrenberg's material can no longer be traced in B.

Graphium nigrum (Berk.) Sacc., Syll. fung. 4: 617. 1886 ≡ *Stilbum nigrum* Berk., *In* Smith, Engl. Fl., Fungi, 2nd ed. 5(2): 330. 1836 (Basionym) [non *S. nigrum* Schard. apud Fr., *nom. nud.*] ≡ *Ceratopordium nigrum* (Sacc.) Kuntze, Rev. Gen. Pl. 2: 847. 1891 ≡ ***Phaeostilbella nigra*** (Berk.) Seifert, **comb. nov., MB 801092.**

Notes: As noted by Seifert (1985), The type specimen (K, *Graphium* folder) is the same as *Phaeostilbella atra* (Desm.) Höhn. The epithet *nigrum* predates the epithet *atra* by two years, and the new combination is thus proposed above. See also *Gr. caliciiforme.*

Graphium nodulosum Marchal & É.J. Marchal, Bull. Soc. Belg. micr. 8: 266. 1894.

Notes: The holotype is not in BR or Gembloux. We have not seen the original diagnosis, which reported an association with *Creonectria laurentiana* (É.J. Marchal) Seaver & Chardón. Despite this, we have no insight on the identity of this fungus.

Graphium obsoletum Sacc., Sylloge 4: 614. 1886 ≡ *Stilbum graphoideum* Berk. & Br., J. Linn. Soc. Bot. 14: 97. 1875.

Notes: No specimens of this fungus are deposited in K, as noted by both Petch (1917) and Seifert (1985). The protologue, which lacks an illustration, is extremely vague. There would be little value in re-introducing this name to the modern literature by neotypification, and we recommend that it be rejected.

Graphium pallescens (Fckl) P. Magn, Hedwigia 44: 375. 1905 ≡ *Stysanus pallescens* Fuckel, Symb. p 102. 1869 ≡ *Harpographium pallesecens* (Fckl) Magnus l.c. p 374.

Notes: Specimens distributed by Fuckel in Herb. Fuckel 1894, and Fungi rhenani are of an inconspicuous, hyaline synnematal fungus with *Cercospora*-like conidiogenous cells and chains of ameroconidia. Morton and Smith (1963) considered the name a *nomen dubium* after failing to find anything other than an *Aspergillus* sp. on the type specimen. Their failure to find the fungus was not surprising given its inconspicuous nature. Braun (1993) considerd this species a synonym of *Phacellium episphaerium* (Desm.) U Braun, and we accept this synonymy here.

Graphium paradoxum Sacc. & Trotter, Bull. Soc. roy. Bot. Belg. 1899: 166, tab E, fig. 11.

Notes: An isotype specimen in BR is of a synnematous *Nodulisporium*. See notes under *Gr. cylindricum*.

Graphium paspali Cif. & Vegni, *In* Vegni, Riv. Patol. veg., Pavia, sér. 3, 3: 209. 1963.

Notes: We have not seen material or the original publication of this species, and cannot comment on its identity.

Graphium passerinii Sacc., Syll. fung. 4: 613. 1886 ≡ *Graphium subulatum* Pass. & Beltrani, Atti R. Acad. Lincei, Trans., sér. 3, 7: 39. 1882 [non *Gr. subulatum* (Nees) Sacc. 1886].

Notes: Saccardo (1886) created this superfluous name because he wanted to create the name *Gr. subulatum* based on *Periconia subulata* Nees (see below).

Graphium pelitnopsis (Corda) Sacc., Syll. fung. 4: 617. 1886 ≡ *Stilbum pelitnopsis* Corda, Icon. Fung. 3: 13. 1839 ≡ *Ceratopodium pelitnopsis* (Corda) Kuntze, Rev. Gen. Pl. 2: 847. 1891.

Notes: Seifert (1985) examined the holotype (PRM 155672) but was unable to completely characterize the fungus; it is neither a true *Graphium* nor a member of the *Ophiostomatale* and may be a basidiomycete similar to *Gr. subinconspicuum,* discussed below.

Graphium perpusillum Sacc. & Traverso, Syll. fung. 19: 796. 1910.

Notes: See *Graphium pusillum* Sacc. [non. (Wallroth) Sacc.] below.

Graphium phycomyces (Auersw.) Sacc., Syll. fung. 4: 614. 1886 ≡ *Hantzschia phycomyces* Auersw., Fungi Eur. no. 411. 1862 ≡ *Leptographium phycomyces* (Auersw.) H. Grossman, Hedwigia 72: 193. 1932 ≡ *Phialocephala phycomyces* (Auersw.) Kendrick, Can. J. Bot. 42: 1292. 1964 ≡ *Kendrickiella phycomyces* (Auersw.) K. Jacobs & M.J. Wing., Can. J. Bot. 79: 113. 2001.

Notes: The lectotype (DAOM 34098) and several isotype specimens (BR, K) that we examined of *H. phycomyces* distributed as Rabenhorst Fungi Europaei 441 corroborate the morphological descriptions of this fungus by Kendrick (1964b) and Jacobs *et al*. (2001b).

Based on DNA sequences, Jacobs *et al.* (2001b) erected a new genus, *Kendrickiella*, with *L. phycomyces* as type species.

Graphium phyllogenum Desm., Annls Sci. nat., Bot., Sér. 3, 16: 297. 1851 ≡ *Graphiothecium phyllogenum* (Desm.) Sacc., Michelia 2: 644. 1882.
Notes: Our examination of an isotype specimen (Fungi Gall. Exs. no. 1781, BR) supports the classification of this species in *Graphiothecium* Fuckel, as revised by Braun (1993).

Graphium piliforme (Pers.) Sacc., Syll. fung. 4: 616. 1886 ≡ *Stilbum piliforme* Pers., Usteris Neue Annanlen 2, Stuck 10: 31. 1794: Fr., Syst. mycol. 3: 303. 1832 ≡ *Ceratopodium piliforme* (Pers.) Kuntze, Rev. Gen. Pl. 2: 847. 1891.
Notes: Contrary to the statement by Seifert (1985), the holotype is in Persoon's herbarium (L.910.263.994), but it is in very poor condition and contains no synnemata representing the original fungus. Although the name was used by early 19th century mycologists, there is little point in reintroducing it to the modern literature through neotypification, and is should be considered for rejection.

Graphium pistillare (Lév.) Sacc., Syll. fung. 4: 615. 1886 ≡ *Stilbum pistillare* Lév., Annls Sci. nat., Bot., Sér. 3, 3: 68. 1845 ≡ *Ceratopodium pistillare* (Lév.) Kuntze, Rev. Gen. Pl. 2: 847. 1891.
Notes: Seifert (1985) was unable to locate the type in PC or G; the diagnosis contains no microscopic measurements. There is little point in reintroducing this name to the modern literature through neotypification, and it should be considered for rejection.

Graphium pistillarioides Speg., Revta Fac. Agron. Vet. Univ. nac. La Plata 2: 254. 1896.
Notes: The holotype material (LPS 33.136) is identical with *Cephalotrichum microsporum* (Sacc.) P.M. Kirk, and the name is thus a taxonomic synonym of that species.

Graphium pruinosipes (Peck) Sacc., Syll. fung. 4: 614. 1886 ≡ *Stilbum pruinosipes* Peck, Ann. Rep. N.Y. St. Mus. nat. Hist. 33: 28. 1883 ('1880') ≡ *Sporocybe pruinosipes* (Peck) Goi., Annali Bot., Roma 21(1): 49. 1935.
Notes: Seifert (1985) considered this a synonym of *Stilbella flavipes* (Peck) Seifert, based on a study of the holotype (NYS).

Graphium pubescens Cooke & Ellis, Grevillea 6: 5. 1887 ≡ *Didymobotryum pubescens* (Cooke & Ellis) Sacc., Syll. fung. 4: 627. 1886 ≡ *Arthrobotryum pubescens* (Cooke & Ellis) Pound & Clem., Minn. bot. Stud. 1, Bull. 9: 728. 1897 ≡ *Phaeoisariopsis pubescens* (Cooke & Ellis) M.B. Ellis, More Dematiaceous Hyphomycetes, p. 234. 1976.
Notes: The holotype (NY) is in poor condition, and cannot be accurately characterized. However, this fungus seems to be a well known pathogen of *Smilax*, and the illustration with the protologue is consistent with the concept of Ellis (1976).

Graphium pusillum (Wallr.) Sacc., Syll. fung. 4: 614. 1886 ≡ *Stilbum pusillum* Wallr., Fl. Crypt. Germ. II: 326. 1833.
Notes: The type is unavailable from STR, but a slide prepared from it (DAOM 44965) is identical with *Cephalotrichum stemonitis* (Pers.) Nees, as noted by Hughes (1958).

Graphium pusillum Sacc., Ann. Mycol. 6: 567. 1908 [*nom. illegit.* Art. 53, non *G. pusillum* (Wallroth) Sacc 1886] ≡ *Graphium perpusillum* Sacc. & Traverso, Syll. fung. 19: 796. 1910.
Notes: Type material (PAD) contains only the *Brachysporium* sp. mentioned as a cohabitant in the protologue. The figure accompanying the protologue is suggestive of a *Graphium* sp., although the conidia are rather large. It would be difficult to convincingly epitypify this name, and we suggest that the name be rejected.

Graphium putredinis (Corda) S. Hughes, Can. J. Bot. 36: 770. 1958 ≡ *Stysanus putredinis* Corda, Icon. Fung. 3: 12. 1839 ≡ *Doratomyces putredinus* (Corda) F.J. Morton & G. Sm., Mycol. Pap. 86: 83. 1968 ≡ *Parascedosporium putredinis* (Corda) M. Lackner & de Hoog, IMA Fungus 2(1): 46. 2011.

Notes: This epithet is currently used for two distinct synnematous hyphomycetes, *Parascedosporium putredinis* (Lackner & de Hoog 2011), the more common application, and *Doratomyces putredinus* (Morton & Smith 1968), less commonly used. Both fungi occurred on the holotype (PRM 155673), which is now in poor condition. KAS examined the holotype in the early 1980s, and found only the white synnemata of the latter species, but a slide (DAOM 40745) prepared by Hughes (1958) and examined by several subsequent authors (including KAS) includes synnemata of both *P. putredinis* and *Cephalotrichum stemonitis,* as well as the aleurioconidial (*Echinobotryum*) synanamorph of the latter species. Corda's illustration (Tab. II, fig. 36) shows synnemata that are far more likely to be *C. stemonitis,* with a more or less ellipsoidal capitulum giving rise to chains of conidia, that either of the two fungi now carrying this epithet. However, Lackner & de Hoog (2011) designated an epitype (CBS 102083), based on JCM 8082, to fix the application of this epithet in *Parascedosporium*. The white synnematous fungus included by Morton & Smith (1968) in *Doratomyces* (now *Cephalotrichum*) therefore requires a new name. A new combination is made here, based on the next oldest available name listed by Morton & Smith (1968): ***Cephalotrichum album*** (Costantin) Seifert, **comb. nov., MycoBank 801065** ≡ *Synpenicillium album* Costantin, Bull. Soc. mycol. Fr. 4: 62. 1888 (Basionym).

Graphium pycnocephalum Grosmann, Z. Parasitenk. 3: 94. 1931.

Descriptions: Grosmann (1931, p. 94); Siemaszko (1939, p. 36, Pl. II Figs 8–9);

Notes: This species is reported as a common associate of *Ips typographus* and other conifer-infesting bark beetles from Northern Europe (Grosmann 1931, Siemaszko 1939, Mathiesen 1950, Mathiesen-Käärik 1954, Kotýnková-Sychrová 1966, Jankowiak 2006, Jankowiak *et al.* 2009). Grossman (1931) did not illustrate his species and the illustrations by Siemaszko (1939) show only undetailed microphotographs of synnemata. The hyaline stipe and yellow spore mass reported by Grossman (1931) are not suggestive of either the *Ophiostomatales* or *Graphium s.str.* The holotype is not in ZT.

Graphium ramosum Preuss, *In* Klotzschii Herb. viv. Mycol. no. 1263. Bot. Zeit. 7: 294. 1949.

Notes: We have not seen the exsiccatus of this fungus, which should be widely distributed. The published diagnosis is too vague to be helpful at suggesting the identity of this species.

Graphium rhizomorpharum (Ces.) Mont., Annls Sci. nat., Bot., Sér. 4, 5: 343. 1856 ≡ *Stilbum rhizomorpharum* Ces., Hedwigia 1: 70. 1855 ≡ *Harpographium rhizomorpharum* (Ces.) Sacc., Syll. fung. 4: 619. 1886 ≡ *Pseudographiella rhizomorpharum* (Ces.) Illman, Rogerson & G. White, Mycologia 77: 665. 1985.

Notes: Seifert (1985) examined Cesati's holotype (RO), confirming the application of this name as the current name for the type species of *Pseudographiella* E.F. Morris.

Graphium rhizophilum Pat., Bull. Soc. mycol. Fr. 4: 126. 1888.

Notes: Based on studies of the holotype (FH) by Seifert (1985), this is a synonym of *Crinula byssogena* (Berk. & Broome) Seifert.

Graphium rhodophaeum Sacc. & Trott., Bull. Acad. R. Sci. Belg., Cl. Sci., sér. 5, 38: 166. 1899.

Notes: Examination of the holotype (BR) by Seifert (1985) demonstrated that this name is a synonym of *Stilbocrea gracilipes* (see above under *Gr. clavulatum*).

Graphium rhodophaeum* var. *elatius Sacc., Ann. mycol. 9: 257. 1911.

Notes: As reported by Seifert (1985, as *Stilbella*), the holotype (PAD) is identical with *Stilbocrea gracilipes* (see above under *Gr. clavulatum*).

Graphium rigidum (Pers.) Sacc., Syll. fung. 4: 610. 1886 ≡ *Stilbum rigidum* Pers., Ann. Bot. (Usteri) 11: 31. 1794.

Notes: Although Seifert (1985) reported that he could find no type material of this species in Persoon's herbarium (L), a slide derived from the type by Hughes (1958) is deposited as DAOM 50951, ex. L 910.264-589. The slide is in poor condition we could not find conidiogenous cells; the size and shape of the conidia and the length of the synnemata are suggestive of the fungus now known as *Exophiala calicioides* (see above). The synonymy will have to remain tentative until the type specimen itself is relocated at L. This name, widely reported in the 19th century literature, was used for a variety of species. The emended concept of Hedgcock (1906), represented by BPI 448820, possibly represents more than one fungus, according to Harrington *et al*. (2001). There is no reason to reintroduce this name into the modern literature by neotypification, and it should probably be proposed for rejection.

Graphium rivulorum (Peyronel) Goid., Annali Bot., Roma 21: 45. 1935 ≡ *Cladographium rivulorum* Peyronel, Nuovo G. bot. ital. 25: 439. 1918.

Notes: The type is not in PAD. This is the type of the hyphomycete genus *Cladographium,* described for a graphium-like fungus with highly penicillate conidiophores. The genus was considered of uncertain status by Seifert *et al*. (2011).

Graphium rubrum Rumbold, Phytopathology 24: 300. 1934.

Notes: SSU sequences from the ex-type strain (CBS 210.34) of this red-spored species, which no longer produces synnemata, placed it among the *Leotiomycetes* (Okada *et al.* 2000; Harrington *et al.* 2001). Harrington *et al*. (2001) considered BPI 448830 to represent the holotype, but did not provide a description or suggest a reclassification for this species. The only other graphium-like anamorphs in the discomycetes are now classified in *Dendrostilbella* (see under *Gr. smaradinum* below).

Graphium saccardoi Peyronel, I germi astmosferici dei fungi con micelio, Diss., Padova: 18. 1913 ≡ *Nematographium saccardoi* (Peyronel) Goid., Annali Bot., Roma 21: 46. 1935.

Notes: The holotype is not in PAD. The fungus was isolated on agar from the air; it cannot be recognized from the description, and the name should not be taken up unless the type can be located.

Graphium sacchari Speg., Revta Fac. Agron. Univ. nac. La Plata 2, no. 19: 253. 1896 ≡ *Graphiopsis sacchari* (Speg.) Goid., Annali Bot., Roma 21: 9. 1935.

Notes: The holotype (LPS 33.137) is identical with *Phaeoisaria clematidis*, as noted by de Hoog and Papendorf (1976).

Graphium samogiticum Motiej. & Alstrup, Nova Hedwigia 83: 250. 2006.

Notes: Like *Gr. aphthosae*, noted above, this species is associated with lichens and probably does not belong to *Graphium s.str.* nor the *Ophiostomatales.* The type will need to be re-examined, and the species will probably be treated in another genus. Its cuneiform, and almost triangular, conidia are distinctive.

Graphium sessile Dearn. & House, Circ. N.Y. St. Mus. 24: 59. 1940 [*nom. inval.*, Art. 36.1]

Notes: This species from leaf spots was validated by Braun (1994), but because it clearly does not belong in *Graphium s.str.*, he described it as *Phacellium sessile* U. Braun.

Graphium silanum Goid., Boll. R. Staz. Patalog. Veget. Roma, N.S. 16: 246. 1937.

Notes: SSU sequences from an isolate from the original collection (CBS 206.37) of this species are very similar to those of *G. rubrum*, placing it among the *Leotiomycetes* (Okada *et* *al.* 2000). However, Harrington *et al.* (2001), whose ITS sequence suggests *Cadophora,* were unconvinced that this isolate actually represented the original material of Goidànich (1937), and the status of the species is thus very uncertain.

Graphium smaragdinum (Alb. & Schw.) Sacc., Syll. fung. 4: 618. 1886 ≡ *Ceratopodium smaragdinum* Alb. & Schw., Consp. Fung., p. 335. 1805 ≡ *Stilbum smaragdinum* Alb. & Schw.: Fr., Sytem. Mycol. 3: 303. 1832 ≡ *Tubercularia smaragdinum* (Alb. & Schw.) Seifert, Stud. Mycol. 27: 127. 1985 ≡ *Dendrostilbella smaragdina* (Alb. & Schw.) Seifert, Stud. Mycol. 45: 185. 2000.

Notes: This relatively common species is currently classified as *Dendrostilbella smaragdina* (*Helotiales*), based on the discovery of a putative undescribed *Claussenomyces* teleomorph (Okada *et al.* 2000).

Graphium socium Sacc., Syll. fung. 4: 613. 1886 ≡ *Graphium tjibodense* Sacc. & P. Syd., Syll. fung. 14: 1111. 1899 ≡ *Pleurographium tjibodense* (Sacc. & P. Syd.) Goid., Annali Bot., Roma 21: 48. 1935.

Notes: There is no holotype in BO or PAD. Although the original description mentions *Gr. socium* as the anamorph of *Peziza stilbum* Fuckel, the later renaming of the fungus as *Gr. tjibodense* mentioned a similarity with “*G. desmazierii”* but with globose conidia, reminiscent of *Drumopama girisa* Subram. However, the contradictory reported associations of *Gr. socium* with a discomycete and a pyrenomycete confuse any speculation about its actual identity in the absence of a type.

Graphium sorbi Peck, Ann. Rep. N.Y. St. Mus. 40: 65. 1887 [non House 1920] ≡ *Phaeoisariopsis sorbi* (Peck) Ouellette & Cauchon, Mycologia 64: 649. 1972.

Notes: The holotype (NYS) is as described by Ouellet & Cauchon (1972); it is a cercosporoid fungus, perhaps more appropriately classified in *Phacellium*. The designation of a neotype by Ouellete & Cauchon (1972) was unjustified, because the species in fully recognizable from the holotype.

Graphium sorbi House, Bull. N.Y. St. Mus.: 63. 1920 [*nom. illegit.* Art. 53.1, non Peck 1887]

Notes: We have not seen the holotype of this illegitimate name, described as the cause of a leaf spot on *Pyrus americana.* The habitat and the description make it very unlikely that this is either a true *Graphium* species or a member of the *Ophiostomatales.*

Graphium sordidiceps Fairm., Proc. Rochester Acad. Sci. 6: 124. 1922.

Notes: We have not seen the original publication of specimens of this fungus, and cannot comment on its identity.

Graphium squarrosum Ellis & Langl., J. Mycol. 6: 36. 1890.

Notes: We have not examined the holotype, which is in BPI. The protologue is suggestive of a species of *Phaeoisaria* or *Harpographium*.

Graphium stercorarium El. March, Bull. Soc. Roy. Bot. Belg. 34: 143. 1895.

Notes: The holotype is not in BR or Gembloux. The habit of this species on dung, and the illustration accompanying the original publication, suggest that it is probably a synonym of *Parascedosporium putredinis*.

Graphium stevensonii (Berk. & Broome) Sacc., Syll. fung. 4: 613. 1886 ≡ *Stilbum stevensonii* Berk. & Broome, Ann. Mag. nat. Hist., Ser. 5, 1: 27. 1878 ≡ *Ceratopodium stevensonii* (Berk. & Broome) Kuntze, Rev. Gen. Pl. 2: 847. 1891.

Notes: Seifert (1985) was unable to accurately characterize the fungus from the holotype (K); it is neither a true *Graphium* nor a member of the *Ophiostomatales.*

Graphium stilboideum Corda, Icon. Fung. 2: 16. 1838 ≡ *Nematographium stilboideum* (Corda) Goid., Annali Bot., Roma 21: 46. 1935.

Notes: No authentic material could be traced in PRM or K. The illustration with the protologue is very suggestive of a member of the *Parascedosporium putredinis* complex.

Graphium strictum Preuss, Linnaea 24: 133. 1851 ≡ *Nematographium strictum* (Preuss) Goid., Annali Bot., Roma 21: 46. 1935.

Notes: There is no type in B, and none is listed by Jülich (1974). The diagnosis is too scanty to allow speculation on the identity of this fungus, and we recommend that the name be rejected rather than neotypified.

Graphium subinconspicuum Corda, Icon. Fung. 2: 16. 1838 ≡ *Stilbum subinconspicuum* (Corda) Bonorden, Handb. Allgem. Mykol., p 137. 1851 ≡ *Botryonipha subinconspicua* (Corda) Kuntze, Rev. Gen. Pl. 2: 845. 1891 ≡ *Stilbella subinconspicua* (Corda) Bres., Ann. mycol. 1: 129. 1903.

Notes: As stated by Seifert (1985), there is no type in Corda’s herbaria (PRM, K). Corda’s illustration is consistent with the usage of this species name by Matsushima (1975), possibly representing one of a complex of common lignicolous species similar to the basidiomycetous teleomorph genus *Stilbotulasnella* Oberw. & Bandoni or the similar anamorph genus *Basidiopycnides* J. Reid, Eyjólfsd. & G. Hausner. See also *Gr. pelitnopsis*.

Graphium subtile Berl., Bull. mycol. Soc. Fr. 8: 111. 1892.

Notes: The holotype is not in PAD and we have not seen the original publication, which includes an illustration. We cannot comment on its possible identity.

Graphium subtile var. ***fructicola*** Ferraris, Fl. ital. crypt. Fungi, Fasc. 13: 864. 1914.

Notes: The holotype is not in PAD. The fungus was described from immature pear fruit from Italy and, if recollected, should be recognizable by its synnemata about 1100 µm tall, and obovate conidia 6-7 x 3–3.5 µm.

Graphium subulatum Pass. & Beltrani, Atti R. Acad. Lincei, Trans., sér. 3, 7: 39. 1882 ≡ *Graphium passerinii* Sacc., Syll. fung. 4: 613. 1886.

Notes: Although there are specimens with this name in the herbaria of Cooke and Grove (K), none are authentic, and we have not found a holotype. No microscopic details are part of the protologue of this fungus found on stalks of *Rubus*, but the subulate stipe terminating with free conidiophores is more suggestive of a *Phaeoisaria* than of a species of true *Graphium.* Saccardo’s superfluous name is discussed above.

Graphium subulatum (Nees) Sacc., Syll. fung. 4: 612. 1886 [*nom. illegit.* Art. 53.1, non Pass. & Beltrani 1882] ≡ *Periconia subulata* Nees, Nova Acta Acad. Leop. Carol. Ac. Naturf. Fo. 9: tab. 5, fig. 8. 1818 ≡ *Stilbum subulatum* (Nees) Spreng., Syst. veg., 16th ed. 4(1): 547. 1827 ≡ *Pachnocybe subulata* (Nees) Berk., *In* Smith, Engl. Fl., Fungi, 2nd ed., 5(2): 333. 1836 ≡ *Ceratopodium subulatum* (Nees) Kuntze, Rev. Gen. Pl. 2: 847. 1891.

Notes: This can be inferred as a synonym of *Cephalotrichum stemonitis*, based on a statement by Corda (1829) that his *Doratomyces neesii*, now considered a synonym of *C. stemonitis* (Morton & Smith 1963), was the same as Nees’s *P. subulata.* To our knowledge, the holotype of Nees has not been re-examined by a modern author.

Graphium tectonae C. Booth, Mycol. Pap. 94: 5. 1964.

Notes: This species was considered a synonym of *Parascedosporium putredinis* (Corda) M. Lackner & de Hoog (Lackner & de Hoog 2011), based on ITS sequences and examination of the ex-type culture (CBS 127.84). We examined the holotype (IMI 95673d) and agree with this conclusion.

Graphium tenuissimum Corda, Icon. Fung. 1: 19. 1837 ≡ *Haplographium tenuissimum* (Corda) Grove, Hardwicke's Science-Gossip 21: 198. 1885 ≡ *Scopularia tenuissima* (Corda) Goid., Annali Bot., Roma 21: 49. 1935.

Notes: The holotype (PRM 155520) contains only a fungus similar to *Cephalotrichum purpureofuscum* (Fr.) S. Hughes. This does not correspond with Corda's original illustration, which is of a mononematous fungus. *Nomen dubium*.

Graphium terricola Manohar., P.Rag. Rao, Rehana & P.Rama Rao, Nova Hedwigia 26: 474. 1975. *nom. inval.* Art. 37.7

Notes: Authentic material (IMI 161970) is in very poor condition, and the original culture was apparently not preserved. The synnemata are extremely tiny and although the oblong conidia are similar to those of the *Gr. penicillioides* complex, no conidiogenous cells were observed. The soil habitat would be unusual for a member of *Graphium* in the strict sense.

Graphium tjibodense Sacc. & P. Syd., Syll. fung. 14: 1111. 1899 ≡ *Graphium socium* Sacc., Syll. fung. 4: 613. 1886 ≡ *Pleurographium tjibodense* (Sacc. & P. Syd.) Goid., Annali Bot., Roma 21: 48. 1935.

Notes: See under *Gr. socium* above.

Graphium trifolii Jaap, Ann. mycol. 9: 340. 1911 ≡ *Phacellium trifolii* (Jaap) U. Braun, Nova Hedwigia 56: 439. 1993.

Notes: Our observations from the holotype (HBG) are consistent with the redisposition of the species in *Phacellium.*

Graphium typhinum (Wallr.) Sacc., Syll. fung. 4: 617. 1886 ≡ *Stilbum typhinum* Wallr., Fl. crypt. Germ. 2: 330. 1833.

Notes: The holotype was unavailable from STR, but slides derived from it (DAOM 49092) are *Cephalotrichum stemonitis* (Pers.) Nees*,* as stated by Hughes (1958).

Graphium umbellatarum Ces., *In* Klotzsch, Bot. Ztg. 11: 237. 1853.

Notes: Authentic material distributed by Rabenhorst (Herb. myc., ed. 1, no. 1750, BR!) is of an unidentifiable species of *Ophiostoma* or *Ceratocystis*. The name has become entangled with *Cenangium umbellatarum* Ces., which is a coincidental epithet based on a different exsiccatum.

Graphium ungerii Sacc., Syll. fung. 15: 53 ≡ *Graphium penicillioides* var. *ungeri* Sacc., Syll. fung. 4: 610. 1886.

Notes: We have not seen the type of this fungus. Saccardo (1886) based his variety on a drawing by Unger (1847), which shows a synnema with dark brown, seta-like hyphae on the outside of the stipe, growing towards the capitulum, reminiscent of the anamorph of *Ophiostoma setosum* or *O. cupulatum*. Examination of Unger's specimen would be required to determine whether this provides an earlier name for one of these species, or whether it is something different.

Graphium verticillatum Speg., An. Soc. Cient. Argent. 13: 31. 1882 ≡ *Ceratopodium verticillatum* (Speg.) Kuntze, Rev. Gen. Plt 2: 847. 1891 ≡ *Graphiopsis verticillata* (Speg.) Goid., Annali Bot., Roma 21: 9. 1935.

Notes: The type specimen (LPS 26.842) contains no identifiable synnematous fungi but the unpublished drawing on the packet suggests a synnematous *Nodulisporium* sp. See notes under *Gr. cylindricum*.

Graphium verticillioides Speg., An. Soc. Cient. Argent. 22: 218. 1886.

Notes: The type specimen, LPS 26.833, is of a synnematous *Nodulisporium* sp. See notes under *Gr. cylindricum*. Hedgcock (1906) emended the species, but Harrington *et al.* (2001) found that the material (BPI 448820) on which Hedgcock (1906) based his emended species description might consist of more than one fungus. Because Spegazzini's material is still available, Hedgcock's emendation is irrelevant and the species should be considered in any future revision of *Nodulisporium.*

Graphium volkartianum Magnus Hedwigia 44: 370. 1905 ≡ *Harpographium volkartianum* Magn., Hedwigia 44: 375. 1905 ≡ *Isariopsis volkartiana* (Magnus) F. Mangenot, Bull. trimest. Soc. mycol. Fr. 74: 139. 1958 ≡ *Phacellium volkartianum* (Magnus) U. Braun, Nova Hedwigia 56: 439. 1993.

Notes: Our observations from the holotype (HBG) are consistent with the reclassification of this species in *Phacellium* by Braun (1993).

Graphium xanthocephalum (Ditmar) Sacc., Syll. fung. 4: 617. 1886 ≡ *Stilbum xanthocephalum* Ditmar, *In* Sturm, Deutschl. Fl., 3 Abt., 1(1): 121. 1817: Fr., Syst. mycol. 3: 303. 1832 ≡ *Ceratopodium xanthocephalum* (Ditm.) Kuntze, Rev. Gen. Pl. 2: 847. 1891.

Notes: The holotype is not in B (Seifert 1985). The fungus cannot be recognized from the protologue. There is no point in reintroducing this name to the modern literature, and it should be considered for rejection.

C.2. EXCLUDED SPECIES DESCRIBED IN OTHER GENERA

Raffaelea barbata (Ellis & Everh.) D. Hawksw., Bull. Br. Mus. Nat. Hist. 6: 272. 1979 ≡ *Fusarium barbatum* Ellis & Everh., J. Mycol. 4: 45. 1888.

Notes: Harrington *et al.* (2010) suggested that this fungus is best treated in *Fusarium* (*Hypocreales*), where it was initially described (Ellis & Everhart 1888), but it is not treated in any of the modern literature on that genus. The illustration by Hawksworth (1979) shows sinuate apices on the conidiogenous cells, perhaps suggestive of species of *Plectophaerella* Kleb.

Ceratocystis buxi (Borissov) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952 ≡ *Ceratostomella buxi* Borissov, USSR Central Forestry Res. Inst. Bull. 2: 7. 1934.

Description: Potlajczuk & Schekunova (1985, pp 155–156).

Notes: According to Hunt (1956), the description of this species is similar to those of *G. penicillata* and *G. serpens*. However, the protologue does not describe any anamorph and shows persistent asci, suggesting this species does not belong to either *Ceratocystis* or any of the genera in the *Ophiostomatales*, but perhaps in *Ceratostomella* where it was initially described.

Raffaelea castellanii (Pinoy) de Hoog, Stud. Mycol. 7: 44. 1974 ≡ *Acladium castellanii* Pinoy, *In* Castellani, British Medical Journal 2910: 486. 1916.

Notes: Excluded from *Raffaelea* by Sutton (1975) and Harrington *et al.* (2010). An ITS sequence (AM492786) produced for the ex-type of this species (CBS 100.26) by Gilgado *et al.* (2008) BLAST to unknown basidiomycetes, while the ITS (HQ185356) and β-tubulin (HQ231813) sequences of the same isolate produced by Lackner & de Hoog (2011), match with those of several isolates of *Scedosporium dehoogii* Gilgado, Cano, Gené & Guarro. The isolate is also stored in MUCL (MUCL 15755), and LSU (EU984260) and SSU (EU294300) sequences produced by Massoumi Alamouti *et al.* (2009) BLAST with more than 97% similarity to *Heleiosa* (*Pleosporales*), while the β-tubulin sequence from the same isolate BLASTs with 90% (HQ231813) *L. elegans* and other *Ophiostoma* spp. Both isolates thus need to be re-assessed to determine whether they still represent the type of *R. castellanii*.

Leptographium costaricense G. Weber, Spaaij & M.J. Wingf., Mycol. Res. 100: 733. 1996.

Notes: The first phylogeny produced for *Leptographium* based on DNA sequences showed that *L. costaricense* grouped somewhat distant from other *Leptographium* spp. (Jacobs *et al.* 2001d). We found that the LSU and ITS2 sequences for *L. costaricense* from that study closely resemble those of *Phialocephala humicola* and *Ph. fusca*. Grünig *et al.*

(2002) produced an ITS phylogeny showing that *Phialocephala* is polyphyletic, and that *Ph. fusca* and *Ph. humicola* do not group with the type species of the genus, *Ph. dimorphospora*, in the *Helotiales* (Wang *et al.* 2006), but in a lineage that they tentatively assigned to the *Lasiosphaeriaceae*. In a more extensive study, Jacobs *et al.* (2003c) suggested with LSU and SSU data that *Ph. fusca* and *Ph. humicola* grouped in the *Ophiostomatales*. However, BLAST results and preliminary analyses of the ITS2 and LSU regions (data not shown) suggest that these three species belong in the *Chaetosphaeriales* with *Ph. fusca* grouping closely to the type species for *Chaetosphaeria*, *Chaetosphaeria innumera*. The sequences of *L. costaricense* and *Ph. humicola* differ only in a few bp and they might actually be one species. If further study confirms this, *L. costaricense* will become a synonym of *Ph. humicola*, the older of the two names (Jong & Davis 1972).

Sporothrix cyanescens de Hoog & G.A. de Vries, Antonie van Leeuwenhoek 39: 515. 1973.
Notes: Currently treated as a species of *Quambalaria* (De Beer *et al.* 2006).

Ophiostoma echinellum (Ellis & Everh.) Syd., *In* Sydow & Sydow, Annls mycol. 17: 43. 1919 ≡ *Ceratostomella echinella* Ellis & Everh., *N. Amer. Pyren.,* p. 195. 1892.
Descriptions: Hedgcock (1906, pp 69–71, Pl. 3 Fig. 3, Pl. 6 Fig. 1); Danilova (1979, p. 137, Fig. 5).
Notes: The species concept was emended by Hedgcock (1906), but it was treated as synonym of *O. piliferum* by Griffin (1968), Olchowecki & Reid (1974), Upadhyay (1981), Hutchison & Reid (1988a) and Seifert *et al.* (1993). Hunt (1956) studied the authentic material (BPI) and concluded that it has persistent asci and thus excluded it from *Ceratocystis*. Danilova (1979) reported *Ceratostomella echinella* from Russia, and also described it with persistent asci. The species was not mentioned in the studies on *Ceratostomella* by Réblóva (2006) and Réblóva & Stepánek (2009).

Sporothrix flocculosa Traquair, L.A. Shaw & Jarvis, Can. J. Bot. 66: 927. 1988.
Notes: *S. flocculosa* is the anamorph of *Pseudozyma flocculosa* (Traquair, L.A. Shaw & Jarvis) Boekhout & Traquair (= *Stephanoascus flocculosus* Traquair, L.A. Shaw & Jarvis) in the Ustilaginales (Boekhout 1995).

Sphaeronaemella fragariae F. Stevens & Peterson, Phytopathology 6: 260. 1916.
Notes: The teleomorph of this species has never been described (Stevens & Peterson 1916). According to Hausner & Reid (2004), Maas (1998) suggested that *S. fragariae* is a synonym of *Phomopsis obscurans* (Ellis & Everh.) B. Sutton. Sequence data of the syntype (CBS 118.16) showed that it groups in the *Diaporthales* (Hausner & Reid 2004; De Beer *et al.* 2012).

Ceratocystis fraxinopennsylvanica T.E. Hinds, *In* Hinds & Davidson, Mycologia 67: 719. 1975.
Notes: Currently treated as *Togninia fraxinopennsylvanica* (T.E. Hinds) Hausner, Eyjólfsdóttir & J. Reid in the *Calosphaeriales* (Hausner *et al.* 1992a; Mostert *et al.* 2003).

Sporothrix fungorum de Hoog & G.A. de Vries, Antonie van Leeuwenhoek 39: 518. 1973.
Notes: The ex-type isolate of this species was shown to produce asci with ascospores in yeastlike culture, and it was thus suggested to be the anamorph of *Stephanoascus farinosus* de Hoog, Rant.-Leht. & M.T. Sm. (Traquair *et al.* 1988).

Viennotidia gliocladiopsifera Matsush., Matsush. Mycol. Mem. 10: 118. 2003 [as *'Viennotidea'*]
Notes: Matsushima (2003) described this species as the teleomorph for *Gliocladiopsis tenuis* (Bugnic.) Crous & M.J. Wingf. Lombard & Crous (2012) showed that the latter species groups in *Gliocladiopsis* (*Nectriaceae*, *Hypocreales*). *V. gliocladiopsifera* should be treated

under the Melbourne Code a synonym of *Gl. tenuis*, and is as such excluded from *Viennotidia*, which is a synonym of *Sphaeronaemella*.

Leptographium hymenaeae A. Ram and C. Ram, Broteria 41: 94. 1972.
Notes: Both Harrington (1988) and Jacobs & Wingfield (2001) questioned the treatment of this species from *Hymenaeae* in Brazil in *Leptographium*. It produces chlamydospores, seta-like structures at the base of the conidiophores, and phialidic conidiogenous cells, all characters not typically associated with *Leptographium* spp.

Sporothrix luteoalba de Hoog, Stud. Mycol. 7: 65. 1974.
Notes: Moore (1987) showed that this species is a Basidiomycete and erected a new genus, *Cerinosterus*, with *S. luteoalba* as type species*.* Middelhoven *et al.* (2000) confirmed that *Cerinosterus* belongs to the *Dacrymycetales.*

Sphaeronaemella macrospora Penz. & Sacc., Malpighia 15: 235. 1902.
Notes: This species is currently treated as *Atractiella macrospora* (Penz. & Sacc.) R.T. Moore (*Atractiellales*, *Pucciniomycotina*) (Oberwinkler & Bandoni 1982; Moore 1987).

Ceratostomella merolinensis Georgev., Mitt. Inst. Forstw. Forsch., Belgrade 16: 17. 1930 ≡ *Ophiostoma merolinense* (Georgev.) Nannf., *In* Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934 ≡ *Ceratocystis merolinensis* (Georgev.) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.
Anamorph: *Graphium.*
Notes: This species produces long cylindrical asci (Georgevitch 1930), was considered as of uncertain status by Hunt (1956), and not mentioned by Upadhyay (1981), Réblóva (2006) or Réblóva & Stepánek (2009).

Ceratostomella microcarpa P. Karst., Hedwigia 23: 86. 1884 ≡ *Ceratocystis microcarpa* (P. Karst.) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.
Anamorph: unknown.
Notes: Hunt (1956) suggested that this species should be excluded from *Ceratocystis* because the protologue described persistent asci, implying that this species cannot be accommodated in the *Ophiostomatales* or *Microascales*. The species was not mentioned in the studies of Upadhyay (1981), Réblóva (2006) and Réblóva & Stepánek (2009). Not to be confused with *Gra. microcarpum* (Yamaoka & Masuya), Z.W. de Beer, Masuya & Yamaoka*.*

Ceratostomella microspora Ellis & Everh., Proc. Acad. Nat. Sci. Phil. 45: 444. 1893.
Notes: Hunt (1956) examined type material and excluded this species from *Ceratocystis* because it has persistent asci. The species was not mentioned in the studies of Réblóva (2006) and Réblóva & Stepánek (2009). Not to be confused with *O. microsporum* Arx (see under *Ophiostoma*, section A.1) or *L. microsporum* R.W. Davidson (see under *Leptographium*, section A.1).

Sporothrix rugulosa Traquair, L.A. Shaw & Jarvis, Can. J. Bot. 66: 929. 1988.
Notes: *S. rugulosa* is the anamorph of *Pseudozyma rugulosa* (Traquair, L.A. Shaw & Jarvis) Boekhout & Traquair (= *Stephanoascus rugulosus* Traquair, L.A. Shaw & Jarvis) in the *Ustilaginales* (Boekhout 1995).

Sporothrix tuberum Fontana & Bonfante, Allionia 17: 12. 1971 [*nom. inval.*, Art. 37.1]
Notes: de Hoog (1974) validated this species but treated it in the genus *Nodulisporum*.

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Table 1. Species names from non-fungal genera that are homonyms of ophiostomatoid genera. *Ceratocystis* Jaekel represents invertebrate fossils, *Ophiostoma* Rudolphi parasitic nematodes, and *Graphium* Scopoli swallowtail butterflies. The application of these names to fungal species are permissable because they are dictated by a different nomenclatural Code, but should preferably be avoided (De Beer *et al.* 2012). Species for which homonyms among the Fungi were already described are marked with *.

Taxon	Reference
***Ceratocystis* Jaekel** (Echinodermata, Stylophora)	Jaekel 1901
Ceratocystis perneri Jaekel	Jaekel 1901
Ceratocystis prosthiakida Rahman, Zamora & Geyer	Rahman *et al.* 2010
Ceratocystis spinosa Ubaghs	Ubaghs 1967
Ceratocystis vizcainoi Ubaghs	Ubaghs 1987
***Graphium* Scopoli** (Lepidoptera, Papilionidae)	
113 species of *Graphium* Scopoli are listed on the following website: www.catalogueoflife.org	
***Ophiostoma* Rudolphi** (Nematoda, Metazoa)	Rudolphi 1809
Ophiostoma amphiacanthum Diesing	Diesing 1851
Ophiostoma bifidum (Fabricius) Zeder	Rudolphi 1809
Ophiostoma cristatum (Froelich, 1802) Rudolphi	Rudolphi 1819
Ophiostoma cystidicola Rudolphi	Rudolphi 1809
**Ophiostoma denticulatum* Rudolphi	Rudolphi 1819
Ophiostoma dispar Rudolphi	Rudolphi 1809
Ophiostoma farionis (Fisch.) Rudolphi	Rudolphi 1809
Ophiostoma lepturum Rudolphi	Rudolphi 1809
Ophiostoma mucronatum Rudolphi	Rudolphi 1809
Ophiostoma phocae Zeder	Rudolphi 1809
Ophiostoma pouterii Cloquet	Cloquet 1822
Ophiostoma rajae (Müll.) Rudolphi	Rudolphi 1809
Ophiostoma sphaerocephalum Rudolphi	Rudolphi 1819
**Ophiostoma spinosum* Willemoes-Suhm	Willemoes-Suhm 1869

Text Box 1: Excerpts from the Code of Nomenclature referred to in the nomenclator
References in the nomenclator to articles of the ICBN (International Code of Botanical Nomenclature) refer to the Vienna Code (McNeill *et al.* 2006), because the newly adopted ICN (International Code of Nomenclature for Algae, Fungi and Plants), which will be referred to in future as the Melbourne Code (Hawksworth 2011, Norvell 2011), was not yet published at the time of going to press. Abbreviations and terminology used in relation to the Code are defined below, followed by a brief interpretation of all articles from the Code to which reference is made in the nomenclator. For taxonomic or technical purposes the reader should consult the latest available version of the Code.

comb. nov. A new binomial formed when a species is transferred from one genus to another (Art 7.4).
***nom. illegit*.** The name is illegitimate and cannot be used or corrected (Art. 52.1, 53.1, 53.3).
***nom. inval*.** The name is invalidly described and should not be used until corrected (Art. 33.4, 36.1, 37.1, 37.6, 37.7).
nom. nov. A new name replacing an illegitimate name that was otherwise validly published (Art. 7.3).
nom. prov. A so-called provisional name published (e.g. in a thesis or a conference abstract) in anticipation that a formal description would be published at a later stage (Art. 34.1).

Art. 9.2. A lectotype is a specimen designated from the original material as the nomenclatural type if no holotype was indicated in the original publication, or if it is missing, or if it is found to belong to more than one taxon.
Art. 9.6. A neotype is a specimen selected to serve as nomenclatural type when the original material has been lost or destroyed, or as long as it is missing.
Art. 9.7. An epitype is a specimen selected to serve as additional material to the type when the holotype, lectotype, or neotype, do not exhibit all the appropriate characters associated with a species. When an epitype is designated, the holotype, lectotype, or neotype that the epitype supports must be explicitly cited.
Notes: In the case of fungi, a living culture is often designated as epitype to serve as source of DNA for molecular studies where the holotype is not in suitable conidtion for DNA exatraction. Under the dual nomenclature system, the discovery of the teleomorph for a species only know by its anamorph, usually implied a new species name with its own nomenclatural type. However, under the Melbourne Code it will be possible that material of a newly discovered state, whether sexual or asexual, be designated as epitype to the existing nomenclatural type, without changes to the species name.
Art. 24.3. Infraspecific names with final epithets such as *typicus* (and others not listed here) purporting to indicate the taxon containing the type of the name of the next higher taxon, are not validly published unless they are autonyms.
Art. 29.1. Before 1 January 2012 publication of a species name is only effective if it was distributed as printed matter to the general public. It was e.g. not effective if merely deposited as a typescript (e.g. a Ph.D. thesis) in a library. According to the Melbourne Code, electronic publication following specific guidelines will be permitted from 1 January 2012 (Knapp *et al*. 2011).
Art. 33.4. On or after 1 January 1953 a new combination is invalid if the basionym (name-bringing or epithet-bringing synonym) for a new combination was not cited explicitly.
Art. 34.1. A so-called provisional name is not validly published when it is merely proposed in anticipation of the future acceptance of the taxon concerned.
Art. 36.1. The name is invalid if it was described without a Latin diagnosis, or without reference to a Latin diagnosis. This article is applicable in its current form to all taxa described between 1 January 1935 and 31 December 2011. The Melbourne Code will allow either Latin or English diagnosis as valid descriptions from 1 January 2012 onwards.
Art. 37.1. A name described after 1 January 1958 is invalid if a type specimen was not explicitly indicated, if the herbarium where it is deposited was not explicitly indicated, or if no species were described in the genus.

Art. 37.6. A name described after 1 January 1990 is invalid if the indication to the type does not include one of the words "typus" or "holotypus", or its abbreviation, or its equivalent in a modern language.

Art. 37.7. A name described after 1 January 1990 is invalid if the single herbarium or institution where the type is conserved is not specified.

Art. 46.2 A name of a new taxon must be attributed to the author or authors to whom both the name and the validating description or diagnosis was ascribed, even when authorship of the publication is different.

Art. 52.1. The name is illegitimate because it is superfluous, meaning that the name has been used before for another taxon.

Art. 53.1. The name is illegitimate because it is a later homonym, i.e. the same name was already used for another taxon in a group covered by the ICBN. This does not extend to names used for animals or bacteria.

Chapter 4

Redefining the genus *Sporothrix*

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Abstract

One of the causal agents of human sporotrichosis, *Sporothrix schenckii*, is the type species for the genus *Sporothrix*. The anamorphs of many species of *Ophiostoma,* including that of its type, *O. piliferum,* have also been treated in *Sporothrix*. During the past 20 years, several studies based on DNA sequences have confirmed that species of *Sporothrix* and *Ophiostoma* converge in the *Ophiostomatales* to form what has been referred to in recent studies as *Ophiostoma sensu lato.* The one fungus one name principles, which is currently being incorporated in the International Code for the Nomenclature of Algae, Fungi and Plants (ICN), dictates that a genus should be defined by the oldest type species included in the genus. If applied to *Ophiostoma sensu lato*, *Sporothrix* would have priority over *Ophiostoma*, resulting in more than 100 new combinations. However, in several recently published phylogenies, it has become clear that the lineage accommodating *S. schenckii*, referred to as the *S. schenckii*-*O. stenoceras* complex, is distinct from *Ophiostoma sensu stricto*, which is defined by *O. piliferum*. The aims of this study were to delineate and redefine the genus *Sporothrix*, to provide new combinations where necessary, and to generate sequence data for as many species as possible in the emended genus, which will serve as standard for future taxonomic studies. Thirty five species of *Ophiostoma* with sporothrix-like anamorphs, together with 17 *Sporothrix* spp. were included. Forty seven of these species were represented by ex-type isolates. Sequences were generated for the ribosomal large subunit (LSU), internal transcribed spacer regions (ITS), beta-tubulin and calmodulin genes. For the latter two regions, the presence or absence of introns was noted, but only exon data were included in the phylogenetic analyses. Our results revealed a monophyletic lineage including 32 taxa that we have defined as *Sporothrix*. This includes the *S. schenckii* complex containing the four human pathogens, all nine species described from *Proteaceae* in Africa, and 10 species occurring on hardwoods. Eleven of the species occur in soil and five have been associated with mites. Only four of the species included in *Sporothrix* are associated with conifer-infesting bark beetles, while by far the majority of the remaining more than 200 known species in the *Ophiostomatales* have such associations. The description of *Sporothrix* was emended to include the sexual states, and nineteen new combinations were provided for species previously treated as *Ophiostoma*. The generic status of an additional 20 *Ophiostoma* and 14 *Sporothrix* spp. could not be resolved satisfactorily. The remaining 24 species of *Sporothrix* have been shown to reside in various other genera.

Taxonomic novelties

Sporothrix abietinum (Marm. & Butin) Z.W. de Beer & M.J. Wingf. comb. nov.; *Sporothrix aurorae* (X.D. Zhou & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. comb. nov.; *Sporothrix candidum* (Kamgan, Jol. Roux & Z.W. de Beer) Z.W. de Beer & M.J. Wingf. comb. nov.; *Sporothrix dentifundum* (Aghayeva & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. comb. nov.;

Sporothrix eucastaneae (R.W. Davidson) Z.W. de Beer & M.J. Wingf. comb. nov.; *Sporothrix fusiforme* (Aghayeva & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. comb. nov.; *Sporothrix gemellus* (Roets, Z.W. de Beer & Crous) Z.W. de Beer & M.J. Wingf. comb. nov.; *Sporothrix gossypinum* (R.W. Davidson) Z.W. de Beer & M.J. Wingf. *comb. nov.; Sporothrix gossypinum* (R.W. Davidson) Z.W. de Beer & M.J. Wingf. *comb. nov.; Sporothrix lunatum* (Aghayeva & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. *comb. nov.; Sporothrix narcissi* (Limber) Z.W. de Beer & M.J. Wingf. *comb. nov.; Sporothrix palmiculminatum* (Roets, Z.W. de Beer & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. comb. nov.; *Sporothrix phasma* (Roets, Z.W. de Beer & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. comb. nov.; *Sporothrix polyporicola* (Constant. & Ryman) Z.W. de Beer & M.J. Wingf. comb. nov.; *Sporothrix proliferum* (Kowalski & Butin) Z.W. de Beer & M.J. Wingf. comb. nov.; *Sporothrix protea-sedis* (Roets, M.J. Wingf. & Z.W. de Beer) Z.W. de Beer & M.J. Wingf. comb. nov.; *Sporothrix rossii* (R.W. Davidson) Z.W. de Beer & M.J. Wingf. nom. nov.; *Sporothrix stenoceras* (Robak) Z.W. de Beer & M.J. Wingf. comb. nov.; *Sporothrix zambiensis* (Roets, M.J. Wingf. & Z.W. de Beer) Z.W. de Beer & M.J. Wingf. comb. nov.

INTRODUCTION

Sporothrix was established more than a century ago when Hektoen and Perkins (1900) presented a detailed case study of a boy who contracted a fungal infection by wounding his finger with a hammer. They isolated and described the fungus for which they provided the binomial *Sporothrix schenckii.* The epithet was derived from the name of B.R. Schenck, who described a similar fungus two years earlier obtained from the infected wounds on an adult man (Schenck 1898). Schenck (1898) suggested that the fungus might be a species of *Sporotrichum*. However, Hektoen and Perkins (1900) applied a new genus name, *Sporothrix*, without providing an explicit generic diagnosis. The genus was thus considered invalid by most subsequent workers who referred to the fungus as *Sporotrichum schenckii* (De Beurmann & Gougerot 1911 and others).

Carmichael (1962) stated that what was referred to as *Sporotrichum schenckii,* did 'not in the least resemble *Sporotrichum aureum*', the type species of the genus *Sporotrichum*, which was later shown to be a basidiomycete (Von Arx 1971; Stalpers 1978). Thus he referred *Sporotrichum schenckii* back to *Sporothrix* (Carmichael 1962)*,* and did not consider it necessary to provide a Latin diagnosis for the genus. Several other authors continued considered *Sporothrix* invalid, but Nicot and Mariat (1973) validated the name with *S. schenckii* as type. De Hoog (1974) accepted their validation in his monograph of the genus, although Domsch *et al.* (1980) regarded the validation unnecessary 'in view of the rather exhaustive *descriptio generico-specifica* (ICBN Art. 42)' by Hektoen and Perkins (1900). Nevertheless, the monograph of De Hoog (1974) was the first thorough treatment in which 12 *Sporothrix* spp. were included and illustrated, together with the anamorphs of 12 species of *Ophiostoma*.

Münch (1907) was the first to refer the anamorphs of some species of *Ophiostoma* (treated in *Ceratostomella* at the time) to the genus *Sporotrichum*. In the previous year, Hedgcock (1906) described the synanamorphs of some *Graphium* spp. also as *Sporotrichum*. Apart from *Sporotrichum*, both Hedgcock (1906) and Münch (1907) applied additional genus names, such as *Cephalosporium* and *Cladosporium,* to variations of the mycelial anamorphs of *Ophiostoma*. Interestingly, most of the subsequent taxonomic works used the latter two genus names when referring to the asexual states of *Ophiostoma* (Lagerberg *et al.* 1927; Melin & Nannfeldt 1934; Siemaszko 1939; Davidson 1942; Bakshi 1950; Mathiesen-Käärik 1953; Hunt 1956). Some authors applied other anamorph genus names including *Cylindrocephalum*, *Hormodendron* (Robak 1932), *Hyalodendron* (Goidánich 1935; Georgescu *et al.* 1948), and *Rhinotrichum* (Georgescu *et al.* 1948; Sczerbin-Parfenenko 1953). In 1968, Barron distinguished between *Sporothrix* and *Sporotrichum*, and suggested that the so-called *Sporotrichum* states described for some *Ceratocystis* (= *Ophiostoma*) species should be referred to *Sporothrix.* In the same year, Mariat and De Bièvre (1968) suggested that *Sporotrichum schenckii* was the anamorph of a species of *Ceratocystis* (= *Ophiostoma*), later specified as *O. stenoceras* (Andrieu *et al.* 1971; Mariat 1971).

De Hoog's (1974) monograph, in which he also listed *S. schenckii* as anamorph of *O. stenoceras*, brought much needed order in the nomenclature of *Ophiostoma* anamorphs. His circumscription of *Sporothrix* accommodated the plasticity of these species that had led to the confusion discussed above. He also appropriately included the anamorphic human pathogens in the same genus as the wood staining fungi and bark beetle associates. Most later authors thus treated anamorphs previously ascribed to all the genera listed above, in *Sporothrix* (Samuels & Müller 1978; Domsch 1980; Upadhyay 1981; De Hoog 1993). Several additional species were also described in *Sporothrix* from a variety of hosts (De Hoog 1978, 1981; Moustafa 1981; De Hoog *et al.* 1985; Constantinescu & Ryman 1985; and more). By the middle 1980's, evidence that *Sporothrix* is not a homogenous group, and that some of the species have basidiomycete affiliations, began to appear (Smith & Batenburg-Van der Vegte 1985; Weijman & De Hoog 1985).

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

During the course of the next decade, increasing numbers of taxa were added to phylogenies of *Ophiostoma*. Thus, the phylogenetic separation between *Ophiostoma s. str.* (including the *O. piceae*, *O. ips* and *O. pluriannulatum* complexes) and what became known as the *S. schenckii-O. stenoceras* complex, became more apparent (De Beer *et al.* 2003; Villarreal *et al.* 2005; Roets *et al.* 2006; Zipfel *et al.* 2006; De Meyer *et al.* 2008; Linnakoski *et al.* 2010; Kamgan Nkuekam *et al.* 2012). This was also evident in the most comprehensive phylogenies of the *Ophiostomatales* to date that included 266 taxa (De Beer & Wingfield 2012). These authors treated the *S. schenckii-O. stenoceras* complex, including 26 taxa producing only sporothrix-like anamorphs, in *Ophiostoma sensu lato*. They also excluded the complex from *Ophiostoma sensu stricto,* which contains several other species with sporothrix-like anamorphs, often in combination with synnematous, pesotum-like anamorphs.

The possibility to link anamorph and teleomorph species and genera based on DNA sequences, as exhibited by the Berbee and Taylor (1992) study, had a major impact on fungal taxonomy and nomenclature. The long-standing debate regarding the impracticality of a dual nomenclature system, that allowed for a single fungus to have different species names for different morphs, culminated in a call for the orderly transition to a single-name nomenclatural system for all fungi (Hawksworth *et al.* 2011). The 18th International Botanical Congress, held in July 2011 in Melbourne, Australia, adopted this resolution, and after 1 January 2013, the newly named International Code of Nomenclature for Algae, Fungi, and Plants (ICN), will allow only one name for one fungus (Hawksworth 2011; Norvell 2011). This means that all names for a single taxon now compete equally for priority, irrespective of the morph that they represent (Hawksworth 2011). If these rules were to be applied indiscriminately and with immediate effect, the taxonomic impacts on *Ophiostoma s.l.* would be immense (De Beer & Wingfield 2012). *Ophiostoma s.l.* as defined by De Beer & Wingfield (2012) includes the *O. ulmi*-, *O. pluriannulatum*-, *O. ips*-, and *S. schenckii-O. stenoceras*-complexes, as well as *O. piliferum* and more than 20 other *Ophiostoma* spp. The new rules dictate that *Sporothrix* as the older name would have priority over *Ophiostoma* (Hektoen & Perkins 1900; Sydow & Sydow 1918). The result would be a redefined *Sporothrix* containing 147 species, 104 of which would require new combinations. These would include well-known tree pathogens such as the Dutch elm disease fungi, *O. ulmi* and *O. novo-ulmi*. To avoid such chaos, De Beer & Wingfield (2012) made several recommendations to be applied in the forseeable future that should ensure nomenclatural stability. One of these was to reconsider the generic status of species complexes such as the *S. schenckii-O. stenoceras*-complex.

DNA sequences allow for species to be delineated more accurately than has been possible using only morphological and biological characters. Typically, more variable gene regions are used for this purpose than for generic level questions as discussed above. During the past decade, sequence data for several gene regions have been employed to delineate closely related species in the *S. schenckii-O. stenoceras*-complex. However, a difficulty has been that medical mycologists working with *S. schenckii* and the other human and animal pathogenic species, have applied different gene regions to distinguish between cryptic species than those used by plant pathologists and generalist mycologists. The latter group have primarily used sequences for the internal transcribed spacer region (ITS) (De Beer *et al.* 2003, Villarreal *et al.* 2005), and/or beta-tubulin (BT) (Aghayeva *et al.* 2004, 2005; Roets *et al.* 2006, 2008, 2010; Zhou *et al.* 2006; De Meyer *et al.* 2008; Linnakoski *et al.* 2010; Madrid *et al.* 2010a; Kamgan Nkuekam *et al.* 2012). In contrast, medical mycologists experimented with several gene regions, including ITS (Galhardo *et al*. 2008), chitin synthase, BT, and calmodulin (CAL) (Marimon *et al.* 2006, 2008). Of these, CAL became the preferred gene region to identify and distinguish between the human pathogenic species (Marimon *et al.* 2007; Madrid *et al.* 2009; Dias *et al.* 2011; Oliveira *et al.* 2011; Romeo *et al.* 2011). A problem that arose, was that in several of the clinical studies, some environmental isolates were included. However, because no CAL sequences are available for the known ‘environmental’ species in *S. schenckii-O. stenoceras*-complex (mostly from wood, soil and *Protea* infructescences), the environmental isolates included in clinical studies could not be accurately identified.

Considering the taxonomic uncertainties surrounding and within the *S. schenckii-O. stenoceras*-complex as outlined above, the aims of the present study were 1) to delineate and redefine the genus *Sporothrix*, 2) to provide new combinations where necessary, and 3) to provide sequence data for as many as possible species in the emended genus, that can serve as standard for future taxonomic studies. To address the genus level questions, we employed the LSU and partial ITS regions, as well as CAL and BT exon data, while recording the presence or absence of introns in the latter two genes. Species level questions were addressed using comparisons of sequence data for the complete ITS regions, as well as CAL and BT data including their introns.

MATERIALS & METHODS

Isolates

Thirty five isolates of *Ophiostoma* spp. with sporothrix-like anamorphs (**Table 1**) that have been mentioned in previous studies as part of the *S. schenckii-O. stenoceras*-complex, were included. An additional 19 isolates representing *Sporothrix* spp. without known teleomorphs were also considered (**Table 1**). Of the total number of 59 isolates, 47 represented the type material of the respective species.

DNA extraction, PCR and DNA sequencing

DNA was extracted following the technique described by Duong *et al.* (2012). The ribosomal LSU region was amplified and sequenced using primers LR3 and LR5 (White *et al.* 1990), while ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990) were used for the ITS regions. The PCR reactions of the BT genes were done using primers T10 (O’Donnell & Cigelnik 1997) and Bt2b, while Bt2a and Bt2b (Glass & Donaldson 1995) were used for sequencing reactions. For the CAL gene primers CL1 and CL2a (O’Donnell *et al*. 2000) were used for most species, but a new primer pair was designed for some *Ophiostoma* spp. that could not be amplified with these primers. The new primers were CL3F (5' - CCGARTWCAAGGAGGCSTTC - 3') and CL3R (5' - TTCTGCATCATRAGYTGSAC - 3'). PCR and sequencing protocols were exactly as described by Duong *et al.* (2012), although the annealing temperature was optimized for some individual reactions.

Phylogenetic analyses

Data sets comprising sequences produced in the present study (**Table 1**) together with reference sequences obtained from NCBI GenBank, were compiled using MEGA 5.0.5 (Tamura *et al.* 2011). The distinct data sets were aligned online using the E-INS-I strategy in MAFFT 6 (Katoh & Toh 2008). The aligned ITS data set was subsequently liberally treated with Gblocks 0.91b (molevol.cmima.csic.es/castresana/Gblocks_server.html) to compensate for substantial variation. Maximum parsimony (MP) was done in MEGA 5.0.5 (Tamura *et al.* 2011), maximum likelihood (ML) using PhyML 3.0 online (Guindon *et al.* 2010), and Bayesian analyses (BI) employing MrBayes 3.1.2 (Ronquist & Huelsenback 2003). The positions of exons in the BT and CAL genes were noted for each species, but intron sequences were excluded from all analyses. The most appropriate substitution models were selected for all four gene regions using the Akaike information criterion (AIC) in ModelTest 3.7 (Posada & Crandall 1998) for ML, and MrModelTest 2 (Nylander 2004) for BI. One thousand bootstrap replicates were performed to determine branch support for trees obtained by MP and ML. For the BI analyses, four independant runs of 5 million generations each were conducted using duplicate Monte Carlo Markov chain searches with four chains. Trees were saved every 100 generations. Burn-in was determined using Tracer 1.4 (http://evolve.zoo.ox.ac.uk/software.html).

RESULTS

Phylogenetic analyses

The numbers of taxa and characters included in each of the four data sets, the selected substitution models, as well as the statistical values resulting from the different analyses, are presented in **Table 2**. Branch support values are presented in the phylogenetic trees (**Figs 1-3**).

The topologies of the phylogenetic trees obtained from the various analyses of the LSU data were similar (**Fig. 1**), with the following genera forming well-supported lineages: *Leptographium sensu lato, Fragosphaeria, Raffaelea sensu stricto, Ophiostoma sensu stricto,* and *Graphilbum*. Most of the *Sporothrix* spp. and *Ophiostoma* spp. with sporothrix-like anamorphs formed one major clade (A, **Fig. 1**) present in all the trees obtained from MP, ML and BI. However, some of the taxa separated in smaller lineages (1 to 7, **Fig. 1**). Lineages 1 and 2 always grouped distinct from, but in proximity of *Ophiostoma s.l.* and *Ceratocystiopsis*. Lineages 3, 4, 5 and 6 did not group consistently in the various analyses. In some trees they grouped peripheral but closest to clade A, while in other trees they grouped within clade A (e.g. lineages 5 and 6, **Fig. 1**). Lineage 3 represented the *O. tenellum* complex as defined by De Beer and Wingfield (2012), but included an additional species, *O. rostrocoronatum*, which was not included in their study. The human pathogenic taxa grouped together in a lineage designated as the *S. schenckii* complex.

The different analyses of the ITS data resulted in topologies exhibiting identical groups (**Fig. 2**). *Ophiostoma s.str.* was well-resolved in all trees. The same taxa that formed clade A in the LSU trees, again grouped together. However, unlike in the LSU trees, lineages 1 to 6 consistently grouped distinct from clade A and *Ophiostoma s.str.* in the ITS trees. An additional lineage (8, **Fig. 2**) representing two taxa not included in the LSU data set, was present amongst lineages 1 to 6. The human pathogenic species again grouped together with good statistical support to form the *S. schenckii* complex. The ITS sequence of *Sporothrix lignivora* (Lineage 7, **Fig. 1**) differed substantially from the other species and was excluded from the ITS data set.

The BT genes of different species presented a variety of intron arrangements (**Table 2** and **Fig. 3**). The BT sequences mostly spanned exons 3, 4, 5, and the 5' part of exon 6. Apart from *O. denticulatum,* which had introns between all these exons, the majority of species had one to two introns missing. Clade A formed a well-supported group based on exon data, and the species in this group had an intron arrangement of either 3/-/5 or -/-/5. Interestingly, species with similar intron arrangements grouped more or less together (groups A1 and A2, **Fig. 3**). Species from lineages 3, 4, 5, and 6 also had an arrangement or 3/-/5, while that of lineages 2 and 7 was 3/4/5 (**Table 2**). Lineage 8 was unique with an arrangement of -/4/5. The trees obtained based on exon data did not fully ditinguish between all the closely related taxa, since much of the variation between species is present in the intron.

The intron arrangements for the CAL gene region were less variable than those of BT, with only two patterns observed (**Table 2** and **Fig. 3**). Group A, together with lineages 2, 4, and 5, had a pattern of 3/4/-, while lineages 1, 3, and 6 presented all three introns (3/4/5). However, the exon data for CAL were more variable than those for of BT and could distinguish between most of the closely related taxa.

DISCUSSION

The results of phylogenetic analyses conducted in this and previous studies have shown that species with sporothrix-like anamorphs do not constitute a monophyletic lineage in the *Ophiostomatales*. The majority of these species group together with *S. schenckii* and the other human pathogenic species in a lineage distinct from *Ophiostoma s. str.* Some of the remaining species producing sporothrix-like anamorphs, including *O. piliferum*, type species of *Ophiostoma*, group in *Ophiostoma s. str.*, together with several species where the sporothrix-like anamorph occurs together with a synnematous synanamorph. The phylogenetic position of an additional 16 species with sporothrix-like anamorphs in the *Ophiostomatales* could not be resolved satisfactorily based on the currently available DNA sequences.

The *S. schenckii* complex

The genus *Sporothrix* is typified by *S. schenckii*, one of only four species in the *Ophiostomatales* regularly associated with human or animal disease (Travassos & Lloyd 1980; Summerbell *et al.* 1980; Barros *et al.* 2011; López-Romero e*t al.* 2011). In our phylogenetic analyses, these species consistently formed a well-supported monophyletic lineage (**Figs 1-3**). They share certain features rather unique to the *Ophiostomatales* (**Table 3**). Apart from *S. luriei,* which is known only from a single clinical isolate, the other species, *S. schenckii*, *S. globosa* and *S. brasiliensis*, have all been isolated from both humans and soil. Furthermore, they all produce small, pigmented blastoconidia in addition to the more commonly occurring , hyaline conidia. This character is shared by only four other species, also found in soil, in the *Ophiostomatales* (**Table 3**). The pigmented blastoconidia thus appear to be an adaptation to survive in the soil, and melanin most probably also allows these opportunistic pathogens to overcome human and animal immune systems, when implanted through trauma in skin or muscle tissue (Dixon *et al.* 1992; Romero-Martinez *et al.* 2000; Morris-Jones *et al.* 2003; Taborda *et al.* 2008; Almeida-Paes *et al*. 2009; Madrid *et al.* 2010b). Other species in the *Ophiostomatales* apparently lack this ability, and despite the fact that they are commonly present on l freshly cut wood in every saw mill, pulp mill and plantation globally, , to the best of our knowledge, only two cases of infections in humans by some of these fungi have been reported (Morelet 1995; Bommer *et al.* 2009).

Distinguishing *Sporothrix* from other *Ophiostomatales*

Our analyses showed that the *S. schenckii* complex forms part of a larger group of species (group A, **Figs 1-3**), including some non-pathogenic *Sporothrix* spp., as well as several *Ophiostoma* spp. Species in this group share certain morphological, ecological and genetic characters that set them apart from the rest of the *Ophiostomatales* (**Table 3**).

Apart from the fact that they all produce sporothrix-like anamorphs, they mostly produce hyaline to white, smooth, apressed cultures, sometime becoming grey or brown with age. The sporothrix-like species in *Ophiostoma s. str*., most notably *O. piliferum* and species in the *O. pluriannulatum* complex, produce cultures that are initially white with masses of fluffy aerial mycelium producing conidia, but soon forming dark grey, brown or black pigmention in the medium, visible when cultures are viewed from below (Upadhyay 1981).

The *Ophiostomatales*, and especially genera such as *Leptographium s. l.* (Harrington & Cobb 1988; Jacobs & Wingfield 2001; De Beer & Wingfield 2012; Linnakoski *et al.* 2012), *Ceratocystiopsis* (Upadhyay 1981; Plattner *et al*. 2009), *Ophiostoma s.l.* (Upadhyay 1981; De Beer & Wingfield 2012) and *Graphilbum* (De Beer & Wingfield 2012), is known primarily as a group of fungi associated with conifer-infesting bark beetles. Some smaller lineages are exceptional in this regard: the *O. ulmi* complex in *Ophiostoma s.l.* and *Fragosphaeria* are staining fungi of hardwoods (De Beer & Wingfield 2012), while *Raffaelea s.l.* is associated with ambrosia beetles infesting both hardwoods and conifers. Apart from the *S. schenckii* complex, species accommodated in group A (**Figs 1-3** and **Table 3**) include 10 species reported only from hardwoods, eight with some association with soil, two from the fruiting bodies of basidiomycetes, and only five species exclusively from conifers, four of which are associated with bark beetles. Of the nine species described from infructescences of *Proteaceae* native to southern Africa, five have been shown to be associated with hyperphoretic mites, and they are also included in group A.

Geographically there are also some patterns in the *Ophiostomatales* that generally correspond to the host associations described above. By far the majority of species have been reported from North America, Europe and Asia (Upadhyay 1981; Jacobs & Wingfield 2001; Plattner *et al*. 2009), where extensive native conifer forests are found. The ophiostomatalean species reported from conifers in the Southern Hemisphere, are almost exclusively found associated with introduced bark beetles on non-native pine species grown in plantations (Zhou et al. 2004, 2006; Thwaites *et al.* 2005). Of the 34 species in group A, 18 have been reported from Africa, 14 from Europe, 11 from North America, six from South America, five from Asia, and two from Australasia. Although there might be a bias towards Africa in terms of sampling, taxa in this group appear to have a broader global distribution than is found in other genera in the *Ophiostomatales*.

Several previous phylogenetic studies have shown good statistical support for the *S. schenckii*-*O. stenoceras* complex (Villarreal *et al.* 2005; Zipfel *et al.* 2006; Linnakoski *et al.* 2010; Madrid *et al.* 2010; Roets *et al.* 2010). The fact that group A did not have strong statistical support in our analyses can be attributed to the inclusion of several additional taxa not included in previous studies, and the variability of the selected gene regions used. However, Zipfel *et al.* (2006) showed consistent patterns in the presence or absence of introns in the BT gene region between different genera and species complexes in the *Ophiostomatales*. This was also clear in our results (**Fig. 3** and **Table 3**). Species in Group A had one of two BT intron arrangements, while all species had a similar intron composition in the CAL gene. Lineages 1 to 8 had various intron arrangements, and apart from lineages 4 and 5, all of them differed from those of group A.

A combination of genetic, mophological, and ecological characters, distinguishes group A from other genera in the *Ophiostomatales*. This group represents the genus *Sporothrix sensu stricto*, which we redefine below, following the one fungus one name principle, to also accommodate species with known teleomorphs previously treated in *Ophiostoma*. New combinations are provided where necessary. The generic placement of species in lineages 1 to 8 in the *Ophiostomatales* was not resolved, and we have chosen to retain their current genus names until more robust data become available to resolve their status. These species are listed below under species of uncertain generic status. Several species previously treated in Sporothrix have been shown in various studies to reside in other genera. These are also listed with a brief explanatory note on their current placement.

TAXONOMY

Sporothrix Hektoen & C.F. Perkins, J. Exp. Med. 5: 80. 1900. **emend.** Z.W. de Beer & M.J. Wingf.
= *Sporotrichopsis* Gueguen, in De Beurmann & Gougerot, Archs Parasit. 15: 104. 1911. [type species *S. beurmannii*; *nom. inval*., Art. 34.1]
= *Dolichoascus* Thibaut & Ansel, in Ansel & Thibaut, Compt. Rend. Hebd. Séances Acad. Sci. 270: 2173. 1970. [type species *D. schenckii*; *nom. inval*., Art. 37.1]
= *Sporothrix* section *Sporothrix* Weijman & de Hoog, Antonie van Leeuwenhoek 51: 118. 1985.
= *Sporothrix schenckii-Ophiostoma stenoceras* complex *sensu* De Beer *et al*., Mycologia 95: 434. 2003.

Ascocarps dark brown to black, bases globose; necks straight or flexuous, cylindrical, tapering slightly to apex, up to 1600 µm long, brown to black; ostiole often surrounded by divergent, ostiolar hyphae, sometimes absent. *Asci* 8-spored, evanescent, globose to broadly clavate. *Ascospores* hyaline, aseptate, lunate, allantoid, reniform, orange section-shaped, sheath absent. *Anamorphs* micronematous, mycelial, hyaline conidia produced holoblastically on denticulate conidiogenous cells. Phylogenetically classified in the *Ophiostomatales*. Beta-tubulin gene lacking intron 4 and in some species also intron 3. Calmodulin gene consistently lacks intron 5.

Type species: *Sporothrix schenckii* Hektoen & C.F. Perkins
Note: The synonymies of *Sporotrochopsis* and *Dolichoascus* with *Sporothrix* are discussed in the Notes accompaning *S. schenckii* below.

Sporothrix abietinum (Marm. & Butin) Z.W. de Beer & M.J. Wingf. **comb. nov.**
≡ *Ophiostoma abietinum* Marm. & Butin, Sydowia 42: 194. 1990. (basionym)
Note: Several isolates of *O. abietinum*, including the ex-type, were treated incorrectly as the *‘O. nigrocarpum* complex*’* by De Beer *et al.* (2003). Aghayeva *et al.* (2004) showed that the two species are distinct, and that De Beer’s isolates all belonged to *O. abietinum*. This species should not be confused with *Leptographium abietinum* (Peck) M.J. Wingf.

Sporothrix africanum G.J. Marais & M.J. Wingf., Mycol. Res. 105: 242. 2001.
= *Ophiostoma africanum* G.J. Marais & M.J. Wingf., Mycol. Res. 105: 241. 2001.

Sporothrix aurorae (X.D. Zhou & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. **comb. nov.**
≡ *Ophiostoma aurorae* X.D. Zhou & M.J. Wingf., Stud. Mycol. 55: 275. 2006. (basionym)

Sporothrix brasiliensis Marimon, Gené, Cano & Guarro, in Marimon *et al.*, J. Clin. Microbiol. 45: 3203. 2007.
Note: Teleomorph not known. *Sporothrix brasiliensis* forms part of the *S. schenckii* complex.

Sporothrix candidum (Kamgan, Jol. Roux & Z.W. de Beer) Z.W. de Beer & M.J. Wingf. **comb. nov.**
≡ ***Ophiostoma candidum*** Kamgan, Jol. Roux & Z.W. de Beer, in Kamgan Nkuekam *et al*., Mycol. Progress 11: 526. 2012. (basionym)

Sporothrix dentifundum (Aghayeva & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. **comb. nov.**

≡ *Ophiostoma dentifundum* Aghayeva & M.J. Wingf., Mycol. Res. 109: 1134. 2005. (basionym)

Sporothrix dimorphospora (Roxon & S.C. Jong) Madrid, Gené, Cano & Guarro, in Madrid *et al*., Mycologia 102: 1199. 2010.

≡ *Humicola dimorphospora* Roxon & S.C. Jong, Can. J. Bot. 52: 517. 1974. (basionym)

Note: Teleomorph not known.

Sporothrix eucastaneae (R.W. Davidson) Z.W. de Beer & M.J. Wingf. **comb. nov.**

≡ *Ceratocystis eucastaneae* R.W. Davidson, Mycologia 70: 856. 1978. (basionym)

Note: *Ceratocystis eucastanea* was treated by Upadhyay (1981), Seifert *et al.* (1993) and De Beer *et al.* (2012) as synonym of *O. stenoceras*. However, our sequences of the ex-type isolate (**Figs 1, 2, 3**) confirmed that this is a distinct species in *Sporothrix*.

Sporothrix fusiforme (Aghayeva & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. **comb. nov.**

≡ *Ophiostoma fusiforme* Aghayeva & M.J. Wingf., Mycologia 96: 875. 2004. (basionym)

Sporothrix gemellus (Roets, Z.W. de Beer & Crous) Z.W. de Beer & M.J. Wingf. **comb. nov.**

≡ *Ophiostoma gemellus* Roets, Z.W. de Beer & Crous, Mycologia 100: 504. 2008. (basionym)

Sporothrix globosa Marimon, Gené, Cano & Guarro, in Marimon *et al.*, J. Clin. Microbiol. 45: 3203. 2007*.*

= *Sporotrichum tropicale* D. Panja, N.C. Dey & L.M. Ghosh, Indian Med. Gaz. 82: 202. 1947. [*nom. inval*., Art. 36.1]

Note: Teleomorph not known. *Sporothrix tropicale* was published without a Latin diagnosis, but the original culture is available in was included in the present study. The species was listed as synonym of *S. schenckii* by De Hoog (1974), but CAL and BT sequences of the ex-type isolate is identical to *S. globosa* isolates (**Fig. 3**), confirming the synonymy. Groups in the *S. schenckii* complex.

Sporothrix gossypinum (R.W. Davidson) Z.W. de Beer & M.J. Wingf. ***comb. nov.***

≡ *Ceratocystis gossypina* R.W. Davidson, Mycologia 63: 12. 1971. (basionym)

≡ *Ophiostoma gossypinum* (R.W. Davidson) J. Taylor, Mycopath. Mycol. Appl. 38: 112. 1976.

Note: Davidson (1971) distinguished between *O. gossypinum* and *C. gossypina var. robusta* (= *S. rossii*, see below) based on perithecium morphology. Upadhyay (1981) treated both species as synonyms of *O. stenoceras*. Hausner & Reid (2003) showed that the LSU sequence of the ex-type isolate (ATCC 18999) of *O. gossypinum* differs from that of *O. stenoceras*. Our results confirmed that the three species are distinct.

Sporothrix humicola de Mey., Z.W. de Beer & M.J. Wingf., Mycologia 100: 656. 2008.

Note: Teleomorph not known.

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

Note: Teleomorph not known. Aghayeva *et al*. (2005) showed that isolates previously treated as *S. lignivora* separated in four clades, one of which represented *S. inflata s. str.* The second group was described as a new species, *S. brunneoviolaceae,* while the third group included the ex-type isolate of *Humicola dimorphospora*, which was transferred to *Sporothrix* by Madrid *et al.* (2010a). The fourth group, designated in our trees a *S. inflata* 2, remains to be described as a new taxon.

Sporothrix lunatum (Aghayeva & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. ***comb. nov.***
≡ *Ophiostoma lunatum* Aghayeva & M.J. Wingf., Mycologia 96: 874. 2004. (basionym)

Sporothrix luriei (Ajello & Kaplan) Marimon, Gené, Cano & Guarro, Med. Mycol. 46: 624. 2008.
≡ *S. schenckii var. luriei* Ajello & Kaplan, Mykosen 12: 642. 1969. (basionym)
Note: Teleomorph not known. Groups in the *S. schenckii* complex.

Sporothrix mexicana Marimon, Gené, Cano & Guarro, in Marimon *et al.*, J. Clin. Microbiol. 45: 3203. 2007.
Note: Teleomorph not known.

Sporothrix narcissi (Limber) Z.W. de Beer & M.J. Wingf. ***comb. nov.***
≡ *Ophiostoma narcissi* Limber, Phytopathology 40: 493. 1950. (basionym)
≡ *Ceratocystis narcissi* (Limber) J. Hunt, Lloydia 19: 50. 1956.

Sporothrix pallida (Tubaki) Matsush., Icon. microfung. Matsush. lect. (Kobe): 143. 1975.
≡ *Calcarisporium pallidum* Tubaki, Nagaoa 5: 13. 1955. (basionym)
= *Sporothrix albicans* S.B. Saksena, Curr. Sci. 34: 318. 1965.
= *Sporothrix nivea* Kreisel & F. Schauer, J. Basic Microbiol. 25: 654. 1985.
Note: Teleomorph not known. *Sporothrix albicans* and *Calcarisporium pallidum* were treated by De Hoog (1974) as synonyms of *S. schenckii*. However, De Meyer *et al*. (2008) showed that these two species formed a single clade with *S. nivea,* distinct from *S. schenckii,* based on BT sequences. *Sporothrix albicans* and *S. nivea* were thus synonymised with *S. pallida*. This synonymy is supported by CAL sequence data produced in the present study (**Fig. 3**).

Sporothrix palmiculminatum (Roets, Z.W. de Beer & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. **comb. nov.**
≡ *Ophiostoma palmiculminatum* Roets, Z.W. de Beer & M.J. Wingf., Stud. Mycol. 55: 208. 2006. (basionym)

Sporothrix phasma (Roets, Z.W. de Beer & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. **comb. nov.**
≡ *Ophiostoma phasma* Roets, Z.W. de Beer & M.J. Wingf., Stud. Mycol. 55: 207. 2006. (basionym)

Sporothrix polyporicola (Constant. & Ryman) Z.W. de Beer & M.J. Wingf. **comb. nov.**
≡ *Ophiostoma polyporicola* Constant. & Ryman, Mycotaxon 34: 637. 1989. (basionym)

Sporothrix proliferum (Kowalski & Butin) Z.W. de Beer & M.J. Wingf. **comb. nov.**
≡ *Ceratocystis prolifera* Kowalski & Butin, J. Phytopathol. 124: 245. 1989. (basionym)
≡ *Ophiostoma proliferum* (Kowalski & Butin) Rulamort, Bull. Soc. Bot. Centre-Ouest, n.s. 21: 511. 1990.

Sporothrix protearum G.J. Marais & M.J. Wingf., Can. J. Bot. 75: 364. 1997.
= *Ophiostoma protearum* G.J. Marais & M.J. Wingf., Can. J. Bot. 75: 363. 1997.

Sporothrix protea-sedis (Roets, M.J. Wingf. & Z.W. de Beer) Z.W. de Beer & M.J. Wingf. **comb. nov.**
≡ *Ophiostoma protea-sedis* Roets, M.J. Wingf. & Z.W. de Beer, Persoonia 24: 24. 2010. (basionym)

Sporothrix rossii (R.W. Davidson) Z.W. de Beer & M.J. Wingf. **nom. nov.**
= *Ceratocystis gossypina var. robusta* R.W. Davidson, Mycologia 63: 13. 1971.

Note: Davidson (1971) distinguished between *O. gossypinum* and *C. gossypina var. robusta* based on perithecium morphology. Subsequent authors treated both species as synonyms of *O. stenoceras* (Upadhyay 1981; Seifert *et al.* 1993). Hausner & Reid (2003) showed that *O. gossypinum* is distinct from *O. stenoceras* based on LSU data. Villarreal (2005) produced an ITS sequence of the ex-type isolate of *C. gossypina var. robusta,* and because this sequence is identical to that of the ex-type of *O. stenoceras*, De Beer & Wingfield (2012) treated *C. gossypina var. robusta* as synonym of *O. stenoceras*. However, BT and CAL sequences produced in the present study clearly distinguished between the taxa (**Fig. 3**), necessitating a new combination for this name. To avoid confusion with *Sporothrix gossypinum* and *Grosmannia robusta* (R.C. Rob. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf. [= *Ophiostoma robustum* (R.C. Rob. & R.W. Davidson) T.C. Harr.], we have designated a new epithet, based on the first name of the original author of this species, Ross W. Davidson. The description for *S. rossii* is the same as the original description of *C. gossypina var. robusta* (Davidson 1971), which is based on the holotype (RWD 609-D = BPI 595661) and ex-type isolate (CBS 116.78 = CMW 1118) from which sequences were obtained for the present study.

Sporothrix schenckii Hektoen & C.F. Perkins, J. Exp. Med. 5: 77. 1900.
= *Sporotrichum beurmannii* Matr. & Ramond, Compt. Rend. Hebd. Séances Mém. Soc. Biol. 2: 380. 1905.
≡ *Sporotrichopsis beurmannii* (Matr. & Ramond) Gueguen, in De Beurmann & Gougerot, Archs Parasit. 15: 104. 1911. [*nom. inval*., Art. 34.1]
≡ *Sporothrix beurmannii* (Matr. & Ramond) Meyer & Aird, J. Infect. Dis. 16: 399. 1915.
≡ for more homotypic synonyms of *S. beurmannii*, see De Hoog (1974, p. 37).
= *Dolichoascus schenckii* Thibaut & Ansel, in Ansel & Thibaut, Compt. Rend. Hebd. Séances Acad. Sci. 270: 2173. 1970. [*nom. inval*., Art. 37.1]
= for more synonyms of *S. schenckii*, see a complete list in De Hoog (1974, p. 37-38).

Note 1: Several synonyms for *S. schenckii* from the medical literature predating 1940, are listed in MYCOBANK and by De Hoog (1974). Those are not listed except for *S. beurmannii* and *D. schenckii* for reasons set out below. Future studies focussing on *S. schenckii* should not ignore the other synonyms for *S. schenckii*.

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

Note 3: *Dolichoascus schenckii*, the type species for *Dolichoascus*, was not validly published (Ansel & Thibaut 1970) because a holotype was not indicated [Art. 34.1] resulting also in an invalid genus name. Ansel & Thibaut (1970) and Thibaut (1972) suggested that *Dolichoascus* (*Endomycetaceae*) represented the sexual stage of *S. schenckii* due to the presence of what they described as endogenous ascospores. However, Mariat & Diez (1971) studied the isolate (CBS 938.72) of Ansel & Thibaut (1970) and argued that the ‘ascospores’ were in fact endoconidia. According to De Hoog (1974), the name *Dolichoascus* could thus not be used for an anamorph genus. The Melbourne Code will allow the use of the name *Dolichoascus* whether a sexual state is present or not, and since the ex-type isolate is still viable, lectotypifcation (Art. 90.2) and validation of the species and genus is possible. However, Marimon *et al.* (2007) produced a CAL sequence for the *D. schenckii* isolate, which showed that it is a synonym of *S. schenckii* (**Fig. 3**). There is thus no need for lectotypification or validation of the species or genus, as *Dolichoascus* would only become a valid synonym for *Sporothrix*.

Note 4: *Sporothrix schenckii* was treated for some years as anamorph of *O. stenoceras* (Taylor 1970, Mariat 1971, De Hoog 1974). However, De Beer *et al.* (2003) showed that the two species were distinct based on ITS sequences, and this was confirmed in the present study with LSU (**Fig. 1**), BT and CAL sequences (**Fig. 3**). No teleomorph is currently known for *S. schenckii*.

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

Sporothrix stenoceras (Robak) Z.W. de Beer & M.J. Wingf. **comb. nov.**
≡ *Ceratostomella stenoceras* Robak, Nyt Mag. Naturvid. Oslo 71: 214. 1932. (basionym)
≡ *Ophiostoma stenoceras* (Robak) Nannf., in Melin & Nannf., Svenska SkogsvFör. Tidskr. 32: 408. 1934.
≡ *Ceratocystis stenoceras* (Robak) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.
= *Ophiostoma albidum* Math.-Käärik, Medd. Skogsforskninginst. 43: 52. 1953.
≡ *Ceratocystis albida* (Math.-Käärik) J. Hunt, Lloydia 19: 48. 1956.
= *Ceratocystis ponderosae* T.E. Hinds & R.W. Davidson, Mycologia 67: 715. 1975.
≡ *Ophiostoma ponderosae* (T.E. Hinds & R.W. Davidson) Hausner, J. Reid & Klassen, Can. J. Bot. 71: 1264. 1993.

Note 1: The anamorph of *O. stenoceras* has often been referred to as *S. schenckii,* but De Beer *et al.* (2003) and data from the present study (**Figs 1, 3**) showed that the two species are distinct.

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

Note 3: De Beer *et al.* (2003) showed that the ex-type of *O. ponderosae* (ATCC 26665 = RWD 900) has identical ITS sequence to *O. stenoceras*. Unfortunately this isolate died in our collection and we could not obtain sequences for the other genes for it. The LSU and ITS sequences of another *O. ponderosae* isolate (CBS 496.77 = RWD 899) from the study of Hinds and Davidson (1975), group in the *O. pluriannulatum* complex (**Figs 1, 2**), but we accept the synonymy of *O. ponderosae* with *O. stenoceras* based on the ITS sequence of the ex-type.

Sporothrix stylites de Mey., Z.W. de Beer & M.J. Wingf., Mycologia 100: 656. 2008.
Note: Teleomorph not known.

Sporothrix variecibatus Roets, Z.W. de Beer & Crous, Mycologia 100: 506. 2008.
Note: Teleomorph not known.

Sporothrix zambiensis (Roets, M.J. Wingf. & Z.W. de Beer) Z.W. de Beer & M.J. Wingf. **comb. nov.**
≡ *Ophiostoma zambiensis* Roets, M.J. Wingf. & Z.W. de Beer, Persoonia 24: 24. 2010. (basionym)

SPECIES WITH SPOROTHRIX-LIKE ANAMORPHS, OF UNCERTAIN GENERIC STATUS IN THE *OPHIOSTOMATALES*

Ophiostoma ambrosium (Bakshi) Hausner, J. Reid & Klassen, Can. J. Bot. 71: 1264. 1993.
≡ *Ceratocystis ambrosia* Bakshi, Trans. Br. Mycol. Soc. 33: 116. 1950. (basionym)
Note: Griffin (1968), Upadhyay (1981), Hutchison & Reid (1988) and Seifert *et al.* (1993) treated *O. ambrosium* as synonym of *O. piliferum*, while Hunt (1956) and De Hoog (1974) treated it as a distinct species. A short LSU sequence of *O. ambrosium* from Hausner *et al.* (1993b) groups with *O. grande* in a lineage (Lineage 1, **Fig. 1**) distinct from *Sporothrix s. str.*

Ophiostoma angusticollis (Wright & Griffin) M. Villarreal, Mycotaxon 92: 262. 2005.
≡ *Ceratocystis angusticollis* Wright & H.D. Griffin, in Griffin, Can. J. Bot. 46: 697. 1968. (basionym)
Note: Our results support those of Villarreal *et al.* (2005) and De Beer & Wingfield (2012) that showed that *O. angusticollis* groups in a lineage (Lineage 2, **Fig. 2**) with *O. sejunctum* and *O. denticulatum* outside of *Sporothrix s.str.*

Ophiostoma bragantinum Pfenning & Oberw., Mycotaxon 46: 381. 1993.
Note: Although LSU sequences place this species within *Sporothrix s. str.* (**Fig. 1**), it grouped with *O. epigloeum* outside that genus based on comparisons of sequences for the other genes (Lineage 5**, Figs 2, 3**). We have thus chosen to treat it in *Ophiostoma s.l.* for the present.

Ophiostoma coronatum (Olchow. & J. Reid) M. Villarreal, Mycotaxon 92: 263. 2005.
≡ *Ceratocystis coronata* Olchow. & J. Reid, Can. J. Bot. 52: 1705. 1974. (basionym)
Note: Upadhyay (1981) treated *O. coronatum* as synonym of *O. tenellum,* but this was rejected by Hutchison & Reid (1988) because of differences in the ascospore shape. Our data support those of Villarreal (2005) and De Beer & Wingfield (2012) that separate the two species. These group together with *O. nigricarpum* and *O. tenellum* in a lineage (Lineage 3, **Figs 1, 2, 3**) at present referred to as the *O. tenellum* complex (De Beer & Wingfield 2012). All the species in this complex differ from those in *Sporothrix s. str.* in that they have CAL intron 5, which lacks in of *Sporothrix s. str.* (**Table 2**).

Ophiostoma denticulatum (R.W. Davidson) Z.W. de Beer, Seifert & M.J. Wingf., in Seifert & Wingfield, *The Ophiostomatoid Fungi*. 2012.
≡ *Ceratocystis denticulata* R.W. Davidson, Mycologia 71: 1088. 1979. (basionym)
Note: De Beer *et al.* (2012) suggested that *O. denticulatum* might belong in the *S. schenckii-O.stenoceras* complex based on morphology. However, this species from ambrosia galleries on *Dendroctonus ponderosae*-killed pines in the USA, groups with *O. sejunctum* and *O. angusticollis* (Lineage 2, **Figs 1, 2, 3**), distinct from *Sporothrix s. str.* It also has intron 4 in its BT gene (**Table 2**), which is absent in all species included in *Sporothrix s. str.*

Ophiostoma epigloeum (Guerrero) de Hoog, Stud. Mycol. 7: 45. 1974.
≡ *Ceratocystis epigloea* Guerrero, Mycologia 63: 921. 1971. (basionym) [as *'epigloeum'*]
Note: Based on LSU sequence (not available in GenBank) *O. epigloeum* grouped with *O. ambrosium*, peripheral to the clade containing species like *S. abietinum* currently treated as *Sporothrix* (Hausner *et al.* 1993b). Based on ITS the species also groups outside of *Sporothrix s. str.,* this time with *O. bragantinum* (Lineage 5, **Fig. 2**).

Ophiostoma fumeum Kamgan, Jol. Roux & Z.W. de Beer, in Kamgan Nkuekam *et al*., Mycol. Progress 11: 527. 2012.

Note: Forms a lineage (Lineage 4, **Figs 1, 2, 3**) distinct from *Sporothrix s. str.*, even though its shares the same BT and CAL intron arrangements as species in that genus (**Table 2**).

Ophiostoma grande Samuels & E. Müll., Sydowia 31: 176. 1978.
Note: This species from *Diatrype* fruiting bodies in Brazil groups with *O. ambrosium* in a lineage (Lineage 1, **Figs 1, 2, 3**) distinct from *Sporothrix s.str*. It also differs from *Sporothrix s. str.* in its arrangement of CAL introns (**Table 2**).

Ophiostoma grandicarpum (Kowalski & Butin) Rulamort, Bull. Soc. Bot. Centre-Ouest, n.s. 21: 511. 1990. [as *'grandicarpa'*]
≡ *Ceratocystis grandicarpa* Kowalski & Butin, J. Phytopathol. 124: 243. 1989. (basionym)
Note: Kowalski and Butin (1989) reported two synanamorphs in their cultures of this species, but according to Seifert *et al.* (1993) these appear to represent the noncatenate and catenate forms of a sporothrix-like anamorph. Based on ITS, this species forms a distinct lineage of uncertain generic affiliation in the *Ophiostomatales*, distinct from *Sporothrix s. str*., but the sequence does not represent the type of the species (De Beer & Wingfield 2012). Sequences should be determined for the ex-type isolate to confirm its position.

Ophiostoma longicollum Masuya, in Masuya *et al.*, Mycoscience 39: 349. 1998.
Note: The morphology of this species from *Quercus* in Japan infested by *Platypus quercivorus,* suggests relatedness with species like *S. stenoceras* or *O. nigricarpum*. Sequence data are needed to confirm its correct phylogenetic placement.

Ophiostoma megalobrunneum (R.W. Davidson & Toole) de Hoog & Scheffer, Mycologia 76: 297. 1984.
≡ *Ceratocystis megalobrunnea* R.W. Davidson & Toole, in Davidson, Hinds & Toole, Mycologia 56: 796. 1964. (basionym)
Note: This species was isolated from oak sapwood in the USA. Ascospore and anamorph morphology suggest that this might be a species of *Sporothrix s. str*., but it should be re-examined and sequenced to confirm.

Ophiostoma nigrogranum Masuya, Mycoscience 45: 278. 2004.
Note: This species from pine in Japan was listed by Masuya *et al.* (2012) as part of the *S. schenckii-O. stenoceras* complex. However, the leptographium- to hyalorhinocladiella-like anamorph and sheathed ascospores suggest an affiliation with *Leptographium s.l.* rather than with *Sporothrix s. str.*

Ophiostoma persicinum Govi & Di Caro, Ann. Speriment. Agraria, n.s. 7: 1644. 1953.
Note: The morphology of this species from peach tree roots in Italy suggests that it belongs in *Sporothrix s. str*. De Beer *et al.* (2012b) could not locate type material for this species and recommended neotypification.

Ophiostoma roraimense Samuels & E. Müll., Sydowia 31: 173. 1978.
Note: LSU and SSU data produced by Hausner *et al.* (1993b) for the ex-type isolate (CBS 351.78) of *O. roraimense* does not group with either the *Ophiostomatales* or *Microascales*. The sequences of *O. roraimense* from the study by Hausner *et al.* (1993b) are not available from GenBank. De Beer & Wingfield (2012) thus retyped the short LSU sequence for the ex-type isolate (CBS 351.78) from the Hausner *et al.* (1993b) paper, and found it had high similarity to several *Pseudozyma* isolates (*Ustilaginales*) in GenBank. Furthermore, the sporodochia with septate conidia (Samuels & Müller, 1978) set this species apart from all known *Ophiostoma* species. Since it is possible that the ex-type

isolates was contaminated by a *Pseudozyma* sp., we recommend re-examination of the holotype and/or ex-type culture to confirm the generic placement of this species.

Ophiostoma nigricarpum (R.W. Davidson) de Hoog, Stud. Mycol. 7: 62. 1974. [as *'nigrocarpum'*]
≡ *Ceratocystis nigrocarpa* R.W. Davidson, Mycopath. Mycol. Appl. 28: 276. 1966. (basionym)
Note: De Beer *et al.* (2003) treated several isolates of *O. abietinum* incorrectly as *O. nigricarpum*. Aghayeva *et al.* (2004) showed that the ex-type isolate of *O. nigricarpum* is distinct from *O. abietinum. O. nigricarpum* forms part of the *O. tenellum* complex (see Note under *O. coronatum*).

Ophiostoma pallidulum Linnakoski, Z.W. de Beer & M.J. Wingf., Persoonia 25: 86. 2010.
Note: Teleomorph not observed. This species with its hyalorhinocladiella-like anamorph grouped close to *O. saponiodorum* in the ITS tree of Linnakoski *et al.* (2010), which on its turn was treated in the *S. schenckii-O. stenoceras* complex. However, in our analyses the two taxa formed a lineage (Lineage 7, Figs 2, 3) distinct from *Sporothrix s. str.*

Ophiostoma rostrocoronatum (R.W. Davidson & Eslyn) de Hoog & Scheffer, Mycologia 76: 297. 1984.
≡ *Ceratocystis rostrocoronata* R.W. Davidson & Eslyn, in Eslyn & Davidson, Mem. N.Y. Bot. Gard. 28: 50. 1976. (basionym)
Note: An ITS sequence produced by Jacobs *et al.* (2003) of the same isolate (CBS 434.77) included in our analyses, grouped with *O. narcissi* (Fig. 2). However, based on the four genes sequenced in the present study (Figs 1-3) and morpholohy, we treat *O. rostrocoronatum* as part of the *O. tenellum* complex (De Beer & Wingfield 2012), designated as Lineage 3 in our analyses (Figs 1, 2, 3). See note under *O. coronatum*.

Ophiostoma saponiodorum Linnakoski, Z.W. de Beer & M.J. Wingf., Persoonia 25: 88. 2010.
Note: This species with its pesotum- to hyalorhinocladiella-like anamorph groups with *O. pallidulum* in a distinct lineage outside of *Sporothrix s. str.* (Lineage 7, Figs 2, 3).

Ophiostoma sejunctum M. Villarreal, Arenal, V. Rubio & M. de Troya, in Villarreal *et al.*, Mycotaxon 92: 260. 2005.
Note: Groups in a distinct lineage with *O. angusticollis* and *O. denticulatum* outside *Sporothrix s. str.* (Lineage 2, Fig. 2).

Ophiostoma tenellum (R.W. Davidson) M. Villarreal, Mycotaxon 92: 263. 2005.
≡ *Ceratocystis tenella* R.W. Davidson, Mycologia 50: 666. 1958. (basionym)
= *Ceratocystis capitata* H.D. Griffin, Can. J. Bot. 46: 699. 1968.
Note: See Note under *O. coronatum*. *Ceratocystis capitata* was treated as a distinct species by Olchowecki and Reid (1974), but suggested to be a synonym of *O. tenellum* by Upadhyay (1981) and listed as such by Villarreal *et al.* (2005) and De Beer *et al.* (2012).

Sporothrix brunneoviolaceae Madrid, Gené, Cano & Guarro, in Madrid *et al*., Mycologia 102: 1199. 2010.
Note: Teleomorph not known. Madrid *et al.* (2010a) described some isolates previously referred to as *S. inflata* by Halmschlager & Kowalski (2003) and Aghayeva *et al*. (2005) as *S. brunneoviolaceae*. Based on LSU it groups in *Sporothrix s. str*. (**Fig. 1**), but it groups outside of that genus based on the other gene regions analysed in the present study (Lineage 6, **Figs 2, 3**). It also differs in its CAL intron arrangement from *Sporothrix s. str.* (**Table 2**). For the present, we do not consider it part of *Sporothrix s. str*., and have choosen not to provide a new combination for it until its generic placement is resolved.

Sporothrix curviconia de Hoog, Stud. Mycol. 7: 33. 1974.
Note: Teleomorph not known. The ex-type isolate (CBS 959.73) from *Terminalia* in the Ivory Coast contains rhamnose in its cell walls, suggesting a placement in the *Ophiostomatales* (Weijman & De Hoog 1985). At present no sequence data are available for this isolate. The ITS, BT and CAL sequences produced in the present study for another isolate (CBS 541.84) labelled as *S. curviconia* from *Pinus radiata* in Chile (**Figs 2, 3**), place this species in *Sporothrix* close to *S. abietinum* and its relatives. However, it is unlikely that an isolate from a tropical hardwood in Africa would be the same as one from introduced pine in Chile, which means that the latter isolate probably represents an undescribed taxon. Thus, the generic placement of the true *S. curviconia* remains unresolved and we have chosen not to provide a new combination for it.

Sporothrix lignivora de Mey., Z.W. de Beer & M.J. Wingf., Mycologia 100: 657. 2008.
Note: Teleomorph not known. This species groups in a lineage of its own (Lineage 8, **Fig. 1**), distinct from *Ophiostoma s. l.* and has been treated as *incertae sedis* in the *Ophiostomatales* by De Beer & Wingfield (2012).

Sporothrix nothofagi Gadgil & M.A. Dick, N. Z. J. For. Sci. 34: 318. 2004.
Note: No sequences are available for this species associated with ambrosia beetles infesting *Nothofagus* in New Zealand. Although the illustrations in the protologue are cryptic, its hardwood host and association with ambrosia beetles suggest an affiliation with *Sporothrix s. str.*

Sporothrix setiphila (Deighton & Piroz.) de Hoog, Stud. Mycol. 7: 32. 1974.
≡ *Calcarisporium setiphilum* Deighton & Piroz., Mycol. Pap. 128: 100. 1972. (basionym)
Note: Teleomorph not known. This species was found overgrowing a *Meliola* fruiting body (De Hoog 1974). Its holotype should be compared to other fungicolous *Sporothrix* spp., but no culture representing the species exists.

SPECIES WITH SPOROTHRIX-LIKE ANAMORPHS, CLASSIFIED IN OTHER GENERA OF THE *OPHIOSTOMATALES*

Sporothrix pirina (Goid.) Morelet, Ann. Soc. Sci. Nat. Arch. Toulon et du Var 44: 110. 1992. [as *'pirinum'*]
Note: Currently treated as synonym of *Ophiostoma catonianum* (Goid.) Goid. in *Ophiostoma s. str.* (De Beer *et al.* 2012; De Beer & Wingfield 2012).

Sporothrix roboris (Georgescu & Teodoru) Grobbelaar, Z.W. de Beer & M.J. Wingf., Mycol. Progress 8: 233. 2009.
Note: Currently treated as synonym of *Ophiostoma quercus* (Georgev.) Nannf. in *Ophiostoma s. str.* (De Beer *et al.* 2012; De Beer & Wingfield 2012).

Sporothrix subannulata Livingston & R.W. Davidson, Mycologia 79: 145. 1987.
Note: Currently treated as synonym of *Ophiostoma subannulatum* Livingston & R.W. Davidson in *Ophiostoma s. str.* (De Beer *et al.* 2012; De Beer & Wingfield 2012).

SPECIES WITH SPOROTHRIX-LIKE ANAMORPHS OF UNCERTAIN GENERIC OR ORDINAL STATUS

Sphaeronema epiglaeum Berk. & M.A. Curtis, in Berkely, Grevillea 2: 84. 1873.
Note: *S. epiglaeum* from *Tremella* fruiting bodies in the USA was considered a synonym of *O. epigloeum* from the same host in Argentina according to Guererro (1971). De Hoog

(1974) suggested the two species were distinct based on the size of the perithecia, but because he could not find ascospores on the type material from Berkely, he did not refer *S. epiglaeum* to a more appropriate genus. The name is valid and should be considered if fresh material can be obtained from the USA.

Sporothrix angkangensis M.Z. Fan, C. Guo & T.Y. Zhang, Acta Mycol. Sinica 9: 137. 1990.
Note: Teleomorph not known. This valid species from the moth *Erranis dira* (Geometridae) in China is well-illustrated in the protologue, but its placement in the *Ophiostomatales* needs to be confirmed with DNA sequences. It is more likely affiliated with the *Cordycipitaceae*.

Sporothrix chondracis B. Huang, M.Z. Fan & Z.Z. Li, in Huang *et al.,* Mycosystema 16: 88. 1997.
Note: Teleomorph not known. Although the origin of this species from a cotton grasshopper in China is unusual, the illustrations in the protologue suggest a true *Sporothrix* species. However, its placement in the *Ophiostomatales* needs to be confirmed with DNA sequences, as it possibly belongs in the *Cordycipitaceae.*

Sporothrix cylindrospora Hol.-Jech., Eesti NSV Tead. Akad. Toim., Biol. seer 29: 144. 1980.
Note: Teleomorph not known. The protologue of this species from *Pinus sibirica* in Turkmenistan could not be obtained for the present study. However, De Hoog *et al.* (1985) and Weijman & De Hoog (1985) studied the type specimen of *S. cylindrospora* and suggested it is similar to *S. luteoalba*, a basidiomycete currently treated in *Cerinosterus* (Moore 1987).

Sporothrix echinospora (Deighton & Piroz.) Katum., *Bull. Faculty of Agriculture, Yamaguchi University* **35**: 108. 1987.
≡ *Calcarisporium echinosporum* Deighton & Piroz., Mycol. Pap. 128: 101. 1972.
Note: Teleomorph not known. This species originates from *Meliola* fruiting bodies in Ghana and was described as a hyperparasite. It produces hyaline and pigmented conidia similar to species like *S. inflata* and *S. brunneoviolaceae*. Its generic placement remains uncertain.

Sporothrix globuligera K. Matsush. & Matsush., Matsush. Mycol. Mem. 8: 52. 1995.
Note: Teleomorph not known. The protologue for this species, listed in www.indexfungorum.org, could not be found in the electronic version of the Matsushima Mycological Memoirs Volumes 1 to 10.

Sporothrix gutturiformis de Hoog, Persoonia 10: 62. 1978.
Note: Sequences produced in the present study for the ex-type isolate of this species from soil in Malaysia, place it in *Sporothrix s.str.* (**Figs 1, 2, 3**). However, according to earlier studies using the same isolate this species shows differences from *S. schenckii* in physiology (De Hoog *et al*. 1985; De Hoog 1993) and septal pore structure (Smith & Batenburg-Van der Vegte 1985). The ex-type isolate thus needs to be reconsidered carefully to determine whether it still corresponds with the original description, before a final generic placement can be made.

Sporothrix inusitatiramosa H.Z. Kong, Acta Mycol. Sin. 10: 129. 1991.
Note: Teleomorph not known. The ex-type culture of this species from wood in China produced a large subunit sequence 100% identical to that of *Gliocladium roseum*. However, the illustrations of the conidiogenous cells in the protologue do not resemble that of *Gliocladium*. The culture should be compared with the holotype to determine whether it still represents the same material.

Sporothrix phellini G.R.W. Arnold, Feddes Repert. Spec. Nov. Regni Veg. 98: 354. 1987.
Note: Teleomorph not known. This species was isolated from a *Phellinus* fruiting body in Cuba. De Hoog (1993) suggested that *S. phellini* might belong with the clavicipitalean *Sporothrix* spp. because it seemingly preferred a chitinous substrate. Several true *Sporothrix* spp. have also been isolated from basidiocarps (**Table 3**), so it possible that this species belongs in *Sporothrix s.str.,* although its septate conidia suggest otherwise.

Sporothrix tardilutea K. Matsush. & Matsush. [as *'tardalutea'*], Matsush. Mycol. Mem. 9: 37. 1996.
Note: Teleomorph not known. The protologue for this species, listed in www.indexfungorum.org, could not be found in the electronic version of the Matsushima Mycological Memoirs Volumes 1 to 10.

SPOROTHRIX SPECIES EXCLUDED FROM THE *OPHIOSTOMALES*

Sporothrix alba (Petch) de Hoog, Stud. Mycol. 7: 22. 1974.
≡ *Sporotrichum album* Petch, Trans. Br. mycol. Soc. 11: 262. 1926. (basionym)
Note: Teleomorph not known. No culture is available for this species from a *Cordyceps* fruiting body on an insect in Sri Lanka (De Hoog 1974). De Hoog (1993) suggested a ‘clavicepitalean relationship.’ The type should be reconsidered and compared with entomopathogenic species such as *Beauveria* (*Cordycipitaceae, Hypocreales*) to confirm its generic placement.

Sporothrix catenata de Hoog & Constant., Antonie van Leeuwenhoek 47: 367. 1981.
Note: Teleomorph not known. The LSU sequence of the ex-type isolate (CBS 215.79) produced in this study is identical to that of *Stephanoascus ciferrii* M.T. Sm., Van der Walt & Johannsen, currently treated as a synonym of *Trichomonascus ciferrii* (M.T. Smith, Van der Walt & Johannsen) Kurtzman & Robnett (*Saccharomycetales*) (Kurtzman & Robnett 2007). This confirms the synonymy of *S. catenata* with *St. ciferrii* suggested by De Hoog & Constantinescu (1981) based on mating compatibility. The ITS, BT and CAL sequences of another isolate (CBS 461.81) labelled as *S. catenata* from the nail of a man in the Netherlands are all identical to the ex-type isolate of *S. nivea* (**Figs 2, 3**), which is currently treated as a synonym of *S. pallida*. The latter isolate should thus be relabelled.

Sporothrix cyanescens de Hoog & G.A. de Vries, Antonie van Leeuwenhoek 39: 515. 1973.
Note: Currently treated as *Quambalaria cyanescens* (de Hoog & G.A. de Vries) Z.W. de Beer, Begerow & R. Bauer (*Microstromatales, Ustilaginomycetes*) (De Beer *et al*. 2006).

Sporothrix eucalypti M.J. Wingf., Crous & W.J. Swart, Mycopathologia 123: 160. 1993.
Note: A Basidiomycete incorrectly described in *Sporothrix* and now known as *Quambalaria eucalypti* (M.J. Wingf., Crous & W.J. Swart) J.A. Simpson (*Microstromatales, Ustilaginomycetes*) (De Beer *et al*. 2006).

Sporothrix flocculosa Traquair, L.A. Shaw & Jarvis, Can. J. Bot. 66: 927. 1988.
Note: *Sporothrix flocculosa* was previously considered the anamorph of *Pseudozyma flocculosa* (Traquair, L.A. Shaw & Jarvis) Boekhout & Traquair (= *Stephanoascus flocculosus* Traquair, L.A. Shaw & Jarvis) in the *Ustilaginales* (Boekhout 1995). Under the Melbourne Code it should be listed as a synonym of *Ps. flocculosa*.

Sporothrix foliorum J.J. Taylor, Mycologia 62: 809. 1970.
Note: Teleomorph not known. Weijman & De Hoog (1985) and De Hoog (1993) treated this species from cabbage leaves in France in *Sporothrix* section *Farinosa,* together with

S. catenata. Our data confirmed that the latter species belongs in the *Saccharomycetales* (see above). It is most likely that *S. foliorum* also belongs in another genus in this order.

Sporothrix fungorum de Hoog & G.A. de Vries, Antonie van Leeuwenhoek 39: 518. 1973.
Note: The ex-type isolate of this species produces asci with ascospores in yeastlike cultures, and it was thus suggested to be a synonym of *Stephanoascus farinosus* de Hoog, Rant.-Leht. & M.T. Sm. (Traquair *et al.* 1988). Weijman & De Hoog (1985) and De Hoog (1993) treated this species in *Sporothrix* section *Farinosa*.

Sporothrix ghanensis de Hoog & H.C. Evans, in De Hoog, Stud. Mycol. 7: 27. 1974.
Note: Teleomorph not known. De Hoog (1993) suggested a 'clavicepitalean relationship' for this species from spider eggs in Ghana.

Sporothrix insectorum de Hoog & H.C. Evans, in De Hoog, Stud. Mycol. 7: 25. 1974.
Note: Teleomorph not known. This species was isolated from insects in Ghana. De Hoog (1993) suggested a 'clavicepitalean relationship'. *Sporothrix insectorum* thus should be compared with species of *Beauveria* to make an accurate generic placement in the *Clavicepitaceae*.

Sporothrix isarioides (Petch) de Hoog, Stud. Mycol. 7: 22. 1974.
≡ *Sporotrichum isarioides* Petch, Trans. Br. mycol. Soc. 16: 58. 1931. (basionym)
Note: Teleomorph not known. As with *S. alba*, this species was found on a *Cordyceps* fruiting body on an insect in Sri Lanka (De Hoog 1974). No culture is available but De Hoog (1974) designated a lectotype and suggested some synonyms not listed here. De Hoog (1993) suggested a 'clavicepitalean relationship'. The lectotype should be re-investigated carefully and compared with *Beauveria* and similar entomopathogenic species to confirm its generic placement.

Sporothrix luteoalba de Hoog, Stud. Mycol. 7: 65. 1974.
Note: This species is currently treated as *Cerinosterus luteoalbus* (de Hoog) R.T. Moore in the *Dacrymycetales* (Moore 1987; Middelhoven *et al.* 2000).

Sporothrix pitereka (J. Walker & Bertus) U. Braun, in Braun, Monogr. *Cercosporella*, *Ramularia* Allied Genera 2: 416. 1998.
Note: Currently treated as *Quambalaria pitereka* (J. Walker & Bertus) J.A. Simpson (*Microstromatales, Ustilaginomycetes*) (De Beer *et al*. 2006).

Sporothrix pusilla U. Braun & Crous, in Braun, Monogr. *Cercosporella*, *Ramularia* Allied Genera 2: 418. 1998.
Note: A Basidiomycete now treated as *Quambalaria pusilla* (U. Braun & Crous) J.A. Simpson (*Microstromatales, Ustilaginomycetes*) (De Beer *et al*. 2006).

Sporothrix ramosissima Arnaud *ex* de Hoog, Stud. Mycol. 7: 28. 1974.
≡ *Gonatobotrys ramosissima* Arnaud, Bull. trimest. Soc. mycol. Fr. 68: 187. 1952.
[*nom. inval.,* Art. 36.1] (basionym)
Note: Teleomorph not known. This species was isolated from moist wood. It differs morphologically from other *Sporothrix* spp. in that it produces branched conidiogenous cells (De Hoog 1974). Weijman & De Hoog (1985) and De Hoog (1993) treated this species in *Sporothrix* section *Farinosa* based on biochemical characters, which were very distinct from those of *S. schenckii* and other ophiostomatalean spp.

Sporothrix ranii Moustafa, Persoonia 11: 392. 1981.
Note: Teleomorph not known. Weijman & De Hoog (1985) and De Hoog (1993) treated this species in *Sporothrix* section *Farinosa* based on biochemical characters, which were very distinct from those of *S. schenckii* and other ophiostomatalean species..

Sporothrix rectidentata (Matsush.) de Hoog, Persoonia 10: 64. 1978.
Note: This species from forest soil in Japan is currently treated as *Engyodontium rectidentatum* (Matsush.) W. Gams, de Hoog, Samson & H.C. Evans.

Sporothrix rugulosa Traquair, L.A. Shaw & Jarvis, Can. J. Bot. 66: 929. 1988.
Note: *S. rugulosa* is the anamorph of *Pseudozyma rugulosa* (Traquair, L.A. Shaw & Jarvis) Boekhout & Traquair (= *Stephanoascus rugulosus* Traquair, L.A. Shaw & Jarvis) in the *Ustilaginales* (Boekhout 1995). Under the Melbourne Code it should be listed as a synonym of *Ps. rugulosa*.

Sporothrix sanguinea C. Ramírez ex J.J. Taylor, Mycologia 69: 651. 1977.
Note: This species from tanning liquors in France is currently treated as *Hyphozyma sanguinea* (C. Ramírez) de Hoog & M.T. Sm.

Sporothrix sclerotialis de Hoog, Persoonia 10: 64. 1978.
Note: Teleomorph not known. This species from the roots of *Lolium perenne* in the Netherlands was treated by Weijman & De Hoog (1985) and De Hoog (1993) in *Sporothrix* section *Farinosa* based on biochemical characters, which were very distinct from those of *S. schenckii* and other ophiostomatalean species.

Sporothrix tuberi Fontana & Bonfante, Allionia 17: 12. 1971. [*nom. inval.*, Art. 37.1] [as *'tuberum'*]
Note: De Hoog (1974) validated this species but treated it in the *Xylariales* as *Nodulisporium tuberum* A. Fontana & Fas.-Bonf. ex de Hoog.

Sporothrix vizei (Berk. & Broome) de Hoog, Persoonia 10: 66. 1978.
Note: Teleomorph not known. This species from sori on ferns was considered as possibly related to the *Clavicepitaceae* by De Hoog (1993). Its septate conidia and branching conidiophores does not resemble any species in *Sporothrix s.str.*

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Table 1 Isolates used in this study. Genbank numbers for sequences obtained in this study are printed in bold type.

								GenBank Accession numbers			
Previous name	**Present name**	**CMW**	**CBS**	**Type**	**Isolated from**	**Country**	**Collector**	**LSU**	**ITS**	**BT**	**CAL**
O. abietinum	*S. abietinum*	22310	125.89	T	*Abies vejari*	Mexico	JG Marmolejo	PENDING	AF484453	PENDING	PENDING
O. africanum	*S. africanum*	823	116571		*Protea gaguedi*	SA	MJ Wingfield	AF221015	DQ316199	DQ296073	
O. albidum	*syn. S. stenoceras*	1123	798.73	T	*Pissodes pini* gallery on *Pinus sylvestris*	Sweden	A Mathiesen-Käärik	PENDING	AF484475	PENDING	PENDING
O. angusticollis	*O. angusticollis*	152	186.86		*Pinus banksiana*	Wisconsin, USA	MJ Wingfield		AY924383		
O. aurorae	*S. aurorae*	19362	118837	T	*Hylastes angustatus* on *Pinus elliottii*	SA	XD Zhou	PENDING	DQ396796	DQ396800	PENDING
O. bragantinum	*O. bragantinum*	17149	474.91	T	virgin forest soil	Brazil	W Gams	PENDING	FN546965	FN547387	PENDING
O. candidum	*S. candidum*	26484		T	*Eucalyptus cloeziana*	SA	G Kamgan Nkuekam	PENDING	HM051409	HM041874	PENDING
O. coronatum	*O. coronatum*	37433	497.77			Canada	RW Davidson	PENDING	AY924385		PENDING
O. denticulatum	*O. denticulatum*	1128	ATCC$^{®}$38087	T	ambrosia gallery *Pinus ponderosa*	Colorado, USA	RW Davidson	PENDING	PENDING	PENDING	PENDING
O. dentifundum	*S. dentifundum*	13016	115790	T	*Quercus* wood	Hungary	C Delatour	PENDING	AY495434	AY495445	PENDING
O. epigloeum	*O. epigloeum*	22308	573.63	T	*Tremella fusiformis*	Argentina	RT Guerrero		PENDING		
O. eucastanea	*S. eucastanea*	1124	424.77	T	canker on *Castanea dentata*	North Carolina, USA	RW Davidson	PENDING	PENDING	PENDING	PENDING
O. fumeum	*O. fumeum*	26813		T	*Eucalyptus* sp.	SA	G Kamgan Nkuekam		HM051412	HM041878	PENDING
O. fumeum	*O. fumeum*	26820			*Eucalyptus* sp.	Zambia	G Kamgan Nkuekam	PENDING			
O. fusiforme	*S. fusiforme*	9968	112912	T	*Populus nigra*	Azerbaijan	D Aghayeva	DQ294354	AY280481	AY280461	PENDING
O. gemellus	*S. gemellus*	23057	121959	T	*Tarsonemus* sp. from *Protea caffra*	SA	F Roets	DQ821531	DQ821560	DQ821554	PENDING
O. gossypinum	*S. gossypinum*	1116	ATCC$^{®}$18999	T	*P. ponderosa*	New Mexico, USA	RW Davidson	PENDING	PENDING	PENDING	PENDING
O. gossypinum var. robusta	*S. rossii*	1118	116.78	T	gallery on *P. ponderosa*	New Mexico, USA	RW Davidson	PENDING	AY924388	PENDING	PENDING
O. grande	*O. grande*	22307	350.78	T	bark	Brazil	RD Dumont	PENDING	PENDING		PENDING
O. lunatum	*S. lunatum*	10563	112927	T	*Carpinus betulus*	Austria	T Kirisits	PENDING	AY280485	AY280466	PENDING
O. narcissi	*S. narcissi*	22311	138.5	T	*Narcissus* sp	Netherlands	DP Limber	PENDING	AF194510	PENDING	PENDING
O. nigricarpum	*O. nigricarpum*	651	638.66	T	*Pseudotsuga menziesii*	USA	RW Davidson	DQ294356	AY280490	AY280480	
O. pallidulum	*O. pallidulum*	23278	128118	T	*H. brunneus* on *P. sylvestris*	Finland	ZW de Beer		HM031510	HM031566	
O. palmiculminatum	*S. palmiculminatum*	20677	119590	T	*Protea repens*	SA	F Roets	DQ316143	DQ316191	DQ316153	PENDING
O. phasma	*S. phasma*	20676	119721	T	*Protea laurifolia*	SA	F Roets	DQ316151	DQ316219	DQ316181	PENDING
O. polyporicola	*S. polyporicola*	5461	669.88	T	*Fomitopsis pinicola*	Sweden		PENDING	PENDING	PENDING	PENDING
O. ponderosae	*syn. S. stenoceras*	37984	ATCC$^{®}$26665	T	*P. ponderosa*	USA	TE Hinds		AF484476		
O. proliferum	*S. proliferum*	37435	251.88	T	*Quercus robur*	Poland	T Kowalski	PENDING	PENDING	PENDING	PENDING
O. protearum	*S. protearum*	1103	116567		*P. caffra*	SA	MJ Wingfield		DQ316203	DQ316165	PENDING
O. protearum	*S. protearum*	1107	116654		*P.caffra*	SA	MJ Wingfield	DQ316145	DQ316201	DQ316163	PENDING
O. protea-sedis	*S. protea-sedis*	28601	124910	T	*P.caffra*	Zambia	F Roets		EU660449	EU660464	

Table 1 (continued) Isolates used in this study. Genbank numbers for sequences obtained in this study are printed in bold type.

								GenBank Accession numbers			
Previous name	**Present name**	**CMW**[a]	**CBS**[b]	**Type**	**Isolated from**	**Country**	**Collector**	**LSU**	**ITS**	**BT**	**CAL**
O. rostrocoronatum	*O. rostrocoronatum*	487	434.77	T	pulpwood chips of hardwoods	USA	RW Davidson	PENDING	AY194509	PENDING	PENDING
O. saponiodorum	*O. saponiodorum*	34945	127078	T	*Ips typographus* on *Picea abies*	Finland	R Linnakoski		HM031507	HM031571	
O. splendens	*S. splendens*	896	116379		*Protea repens*	SA	F Roets	AF221013	DQ316205	DQ316167	PENDING
O. stenoceras	*S. stenoceras*	3202	237.32	T	pine pulp	Norway	H Robak	DQ294350	AY484462	AY280471	PENDING
O. tenellum	*O. tenellum*	37439	189.86		*Pinus banksiana*	Wisconsin, USA	MJ WIngfield	PENDING	AY934523	PENDING	PENDING
O. zambiensis	*S. zambiensis*	28604	124912	T	*Protea caffra*	Zambia	F Roets		EU660453	EU660473	
S. albicans	*syn. S. pallida*	17203	302.73	T	soil	England	SB Saksena	PENDING	PENDING	EF139108	AM398396
S. brasiliensis	*S. brasiliensis*	29127	120339	T	human skin	Brazil		PENDING		AM116946	AM116899
S. brunneoviolacea	*S. brunneoviolacea*	37443	124561	T	soil	Spain	H Madrid	PENDING	FN546959	FN547385	PENDING
S. catenata	*S. pallida*	17161	215.79	T	calf skin	Romania		PENDING	PENDING	PENDING	PENDING
S. catenata	*Trichomonascus ciferrii*	17162	461.81		nail of man	Netherlands	GS de Hoog		PENDING	PENDING	PENDING
S. curviconia	*Sporothrix sp.*	17163	541.84		*Pinus radiata* log	Chile	HL Peredo	PENDING	PENDING	PENDING	PENDING
S. dimorphospora	*S. dimorphospora*	12529	553.74	T	soil	Canada	RAA Morall	PENDING	AY495428	AY495439	
S. globosa	*S. globosa*	29128	120340	T	human face	Spain	C Rubio	PENDING	FN549905	AM116966	AM166908
S. guttuliformis	*S. guttuliformis*	17167	437.76	T	soil	Malaysia	T Furukawa	PENDING	PENDING	PENDING	PENDING
S. humicola	*S. humicola*	7618	118129	T	soil	SA	HF Vismer	EF139114	AF484472	EF139100	PENDING
S. inflata 2	*Sporothrix sp.*	12526	156.72		greenhouse soil	Netherlands	H Kaastra-Howeler		AY495425	AY495436	
S. inflata s.str.	*S. inflata s.str.*	12527	239.68	T	wheat field soil	Germany	W Gams	DQ294351	AY495426	AY495437	
S. lignivora	*S. lignivora*	18600	119148	T	*Eucalyptus* utility poles	SA	EM de Meyer	EF139119	EF127890	EF139104	
S. luriei	*S. luriei*	17210	937.72	T	human skin	SA	H Lurie	PENDING	AB128012	AM747289	AM747302
S. mexicana	*S. mexicana*	29129	120341	T	soil, rose tree	Mexico	A Espinosa	PENDING	FN549906	AM498344	AM398393
S. nivea	*syn. S. pallida*	17168	150.87	T	sediment in water purification plant	Germany	G Teuscher, F Schauer	PENDING	EF127879	EF139109	PENDING
S. pallida	*S. pallida*	17209	131.56	T	*Stemonitis fusca*	Japan	K Tubaki	EF139121	EF127880	EF139110	PENDING
S. stylites	*S. stylites*	14543	118848	T	pine utility poles	SA	EM de Meyer	EF139115	EF127883	EF139096	PENDING
S. tropicale nom. inval.	*syn. S. globosa*	17204	292.55	T	human	India	LM Gosh	PENDING		PENDING	AM490354
S. variecibatus	*S. variecibatus*	23051	121961	T	*Trichouropoda* sp. from *Protea repens*	SA	F Roets	DQ821537	DQ821568		PENDING
S. variecibatus	*S. variecibatus*	23060	121960		*Protea longifolia*	SA	F Roets		DQ821569	DQ821573	
S. schenckii	*S. schenckii*	29351	359.36	T	human	USA	JD Davis	PENDING	PENDING	AM114872	AM117437

[a] CMW = Culture Collection of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa.

[b] CBS = Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands ; ATCC = Culture Collection of TC Harrington, Department of Plant Pathology, Iowa State University, Ames, Iowa, USA.

T = ex-type isolates.

Table 2 Parameters used and statistical values resulting from the different phylogenetic analyses of individual datasets.

	Dataset	LSU	ITS	BT	CAL
No. of taxa		118	83	50	49
No. of characters	**Total**	714	292	219	288
MP	**PIC**	181	54	40	52
	No. of trees	67	2187	128	812
	Tree length	757	195	146	172
	CI	0.385	0.469	0.433	0.512
	RI	0.817	0.883	0.725	0.714
ML & BI	**Subst. model**	TrN+G	GTR+I+G	GTR+I+G	TrN+I+G
	Gamma	0.198	0.248	0.618	1.941
	P-inv	-	0.394	0.46	0.613
BI	**Burn-in**	100	100	100	500

PIC = number of parsimony informative characters; CI = consistency index; RI = retention index; Subst. model = best fit substitution model; Gamma = gamma distribution shape parameter; P-inv = proportion of invariable sites.

Table 3 A comparative summary of morphological, ecological, and genetic characters of species of the *Ophiostomatales* (excluding *Ophiostoma s.str.*) with sporothrix-like anamorphs

Group	Species	Teleomorph	Conidia	Colony	Pathogen/Soil	Host	Beetle/mite	BT Introns	CAL Introns	Continent
Sporothrix s.str.	*S. abietinum*	y	h	w		c	bb	?/-/5	3/4/-	Africa, Asia, Australasia, Europe, North America
	S. africanum	y	h	w		p		?/-/5		Africa
	S. aurorae	y	h	h-w	s	c	bb	-/-/5	3/4/-	Africa
	S. brasiliensis	n	h,p	?	p, s			3/-/5	3/4/-	South America
	S. candidum	y	h	w		h		3/-/5	3/4/-	Africa
	S. dentifundum	y	h	h-w		h		3/-/5	3/4/-	Europe
	S. dimorphospora	n	h,p	w	s			3/-/5	3/4/-	Europe, North America, South America
	S. eucastanea	y	h	w		h		?/-/5	3/4/-	North America
	S. fusiforme	y	h	w		h		?/-/5	3/4/-	Asia, Europe
	S. gemellus	y	h	w		p	m	3/-/5	3/4/-	Africa
	S. globosa	n	h,p	?	p, s	reed		3/-/5	3/4/-	Asia, Europe, North America, South America
	S. gossypinum	y	h	w		c	bb	?/-/5	3/4/-	North America
	S. humicola	n	h	w	s			?/-/5	3/4/-	Africa
	S. inflata s.s.	n	h,p	g	s			3/-/5		Europe
	S. lunatum	y	h	w		h		?/-/5	3/4/-	Europe
	S. luriei	n	h	w	p			3/-/5	3/4/-	Africa
	S. mexicana	n	h,p	?	p, s			3/-/5	3/4/-	Europe, North America
	S. narcissi	y	h	w	s	bulbs		?/-/5	3/4/-	Australasia, Europe, North America
	S. pallida	n		w		f		?/-/5	3/4/-	Asia, Europe
	S. palmiculminatum	y	h	h-w		p	m	3/-/5	3/4/-	Africa
	S. phasma	y	h	h-w		p	m	-/-/5	3/4/-	Africa
	S. polyporicola	y	h	br		f		3/-/5	3/4/-	Europe
	S. proliferum	y	h	w		h		-/-/5	3/4/-	Europe
	S. protearum	y	h	w		p		?/-/5	3/4/-	Africa
	S. protea-sedis	y	h	w		p		3/-/5		Africa
	S. rossii	y	h	w		c	bb	?/-/5	3/4/-	North America
	S. schenckii	n		br	p	h			3/4/-	Africa, Europe, North America, South America
	S. splendens	y	h	w		p	m	-/-/5	3/4/-	Africa
	S. stenoceras	y	h	h-w-br	s	h,c		?/-/5	3/4/-	Africa, Asia, Australasia, Europe, North America, South America
	S. stylites	n	h	w		h,c		?/-/5	3/4/-	Africa
	S. variecibatus	n		w		p	m	3/-/5	3/4/-	Africa
	S. zambiensis	y	h	w		p		-/-/5		Africa

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

Table 3 (continued) A comparative summary of morphological, ecological, and genetic characters of species of the *Ophiostomatales* (excluding *Ophiostoma s.str.*) with sporothrix-like anamorphs

Group	Species	Teleomorph	Conidia	Colony	Pathogen/Soil	Host	Beetle/mite	BT Introns	CAL Introns	Continent
Lineage 1	*O. ambrosium*	y	h	h-g		h	ab			Europe
	O. grande	y	h	w		f			3/4/5	South America
Lineage 2	*O. angusticollis*	y	h	h-w		c				North America
	O. denticulatum	y	h	w-br		c	ab	3/4/5	3/4/-	North America
	O. sejunctum	y	h	h-w		c	bb			Europe
Lineage 3	*O. coronatum*	y	h	w		c			3/4/5	North America
	O. nigricarpum	y	h	h		c	bb	3/-/5		North America
	O. rostrocoronatum	y	h	w		h		3/-/5	3/4/5	Australasia, North America
	O. tenellum	y	h	w-b		c	bb	?/-/5	3/4/5	North America
Lineage 4	*O. fumeum*	y	h	g		h	c	3/-/5	3/4/-	Africa
Lineage 5	*O. bragantinum*	y	h,p	h	s			3/-/5	3/4/-	South America
	O. epigloeum	y	h	h-w		f				South America
Lineage 6	*S. brunneoviolacea*	n	h,p	w, g	s			3/-/5	3/4/5	Europe
Lineage 7	*O. pallidulum*	y	h	h-w		c	bb	?/4/5		Europe
	O. saponiodorum	y	h	h-w		c	bb	?/4/5		Europe
Lineage 8	*S. lignivora*	n	h	olivaceous		h		-/4/5		Africa

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

Fig. 1 Phylogram resulting from ML analyses of the LSU sequences of species representing all the genera in the *Ophiostomatales*. Coloured blocks marked numerically indicate lineages containing *Sporothrix* spp. or *Ophiostoma* spp. with sporothrix-like anamorphs not forming part of any well-defined genus. T indicates ex-type isolates. Significant support values for branches are indicated by bold lines in shades of grey.

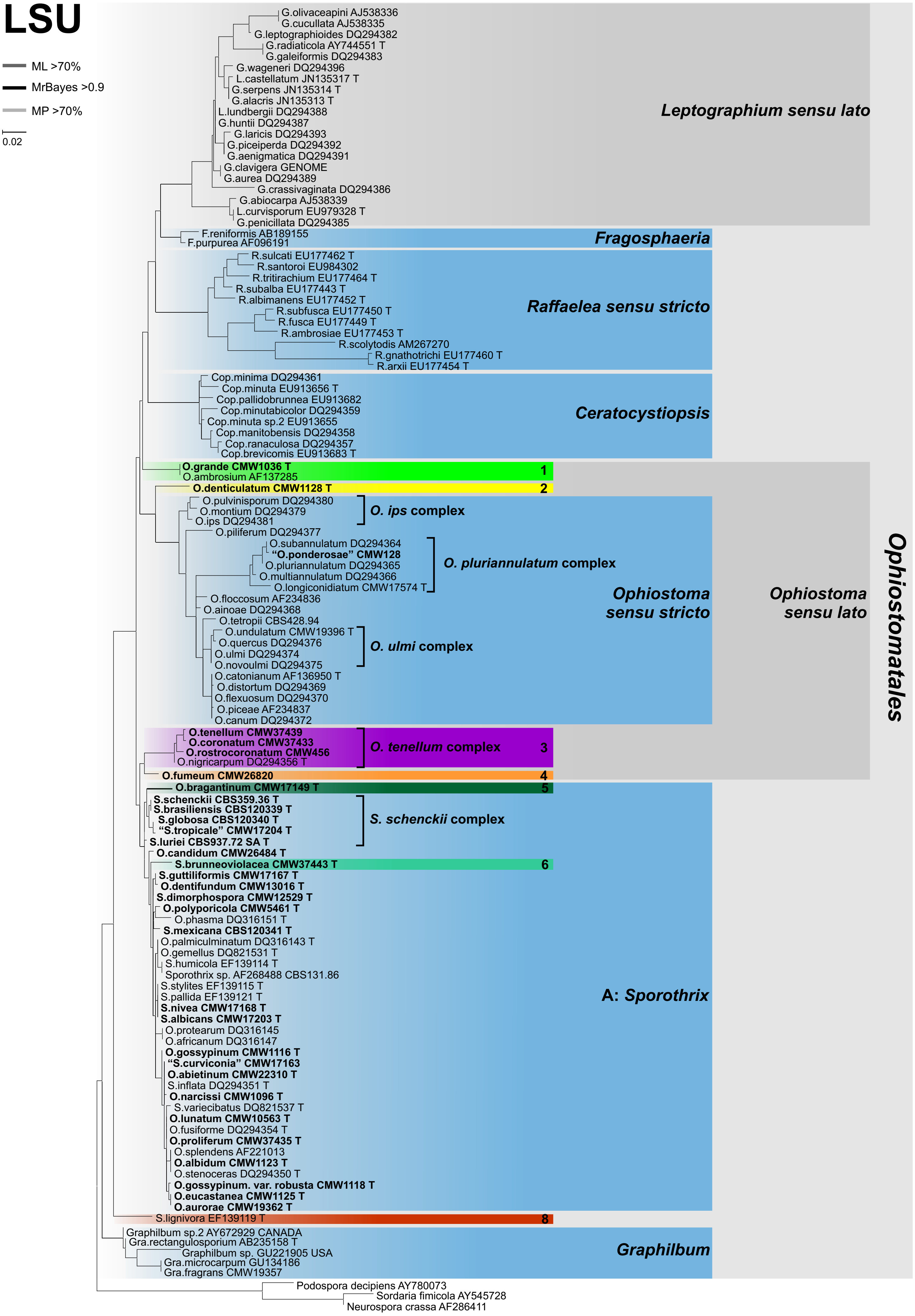

LSU
ML >70%
MrBayes >0.9
MP >70%
0.02
G.olivaceapini AJ538336
G.cucullata AJ538335
G.leptographioides DQ294382
G.radiaticola AY744551 T
G.galeiformis DQ294383
G.wageneri DQ294396
L.castellatum JN135317 T
G.serpens JN135314 T
G.alacris JN135313 T
L.lundbergii DQ294388
G.huntii DQ294387
G.laricis DQ294393
G.piceiperda DQ294392
G.aenigmatica DQ294391
G.clavigera GENOME
G.aurea DQ294389
G.crassivaginata DQ294386
G.abiocarpa AJ538339
L.curvisporum EU979328 T
G.penicillata DQ294385
Leptographium sensu lato
F.reniformis AB189155
F.purpurea AF096191
Fragosphaeria
R.sulcati EU177462 T
R.santoroi EU984302
R.tritirachium EU177464 T
R.subalba EU177443 T
R.albimanens EU177452 T
R.subfusca EU177450 T
R.fusca EU177449 T
R.ambrosiae EU177453 T
R.scolytodis AM267270
R.gnathotrichi EU177460 T
R.arxii EU177454 T
Raffaelea sensu stricto
Cop.minima DQ294361
Cop.minuta EU913656 T
Cop.pallidobrunnea EU913682
Cop.minutabicolor DQ294359
Cop.minuta sp.2 EU913655
Cop.manitobensis DQ294358
Cop.ranaculosa DQ294357
Cop.brevicomis EU913683 T
Ceratocystiopsis
O.grande CMW1036 T
O.ambrosium AF137285
1
O.denticulatum CMW1128 T
2
O.pulvinisporum DQ294380
O.montium DQ294379
O.ips DQ294381
O. ips complex
O.piliferum DQ294377
O.subannulatum DQ294364
"O.ponderosae" CMW128
O.pluriannulatum DQ294365
O.multiannulatum DQ294366
O.longiconidiatum CMW17574 T
O. pluriannulatum complex
O.floccosum AF234836
O.ainoae DQ294368
O.tetropii CBS428.94
O.undulatum CMW19396 T
O.quercus DQ294376
O.ulmi DQ294374
O.novoulmi DQ294375
O. ulmi complex
O.catonianum AF136950 T
O.distortum DQ294369
O.flexuosum DQ294370
O.piceae AF234837
O.canum DQ294372
Ophiostoma sensu stricto
Ophiostoma sensu lato
Ophiostomatales
O.tenellum CMW37439
O.coronatum CMW37433
O.rostrocoronatum CMW456
O.nigricarpum DQ294356 T
O. tenellum complex
3
O.fumeum CMW26820
4
O.bragantinum CMW17149 T
5
S.schenckii CBS359.36 T
S.brasiliensis CBS120339 T
S.globosa CBS120340 T
"S.tropicale" CMW17204 T
S.luriei CBS937.72 SA T
S. schenckii complex
O.candidum CMW26484 T
S.brunneoviolacea CMW37443 T
6
S.guttiliformis CMW17167 T
O.dentifundum CMW13016 T
S.dimorphospora CMW12529 T
O.polyporicola CMW5461 T
O.phasma DQ316151 T
S.mexicana CBS120341 T
O.palmiculminatum DQ316143 T
O.gemellus DQ821531 T
S.humicola EF139114 T
Sporothrix sp. AF268488 CBS131.86
S.stylites EF139115 T
S.pallida EF139121 T
S.nivea CMW17168 T
S.albicans CMW17203 T
O.protearum DQ316145
O.africanum DQ316147
O.gossypinum CMW1116 T
"S.curviconia" CMW17163
O.abietinum CMW22310 T
S.inflata DQ294351 T
O.narcissi CMW1096 T
S.variecibatus DQ821537 T
O.lunatum CMW10563 T
O.fusiforme DQ294354 T
O.proliferum CMW37435 T
O.splendens AF221013
O.albidum CMW1123 T
O.stenoceras DQ294350 T
O.gossypinum. var. robusta CMW1118 T
O.eucastanea CMW1125 T
O.aurorae CMW19362 T
A: Sporothrix
S.lignivora EF139119 T
8
Graphilbum sp.2 AY672929 CANADA
Gra.rectangulosporium AB235158 T
Graphilbum sp. GU221905 USA
Gra.microcarpum GU134186
Gra.fragrans CMW19357
Graphilbum
Podospora decipiens AY780073
Sordaria fimicola AY545728
Neurospora crassa AF286411

Fig. 2 Phylogram resulting from ML analyses of the ITS sequences (treated with GBlocks) of species representing genera in the *Ophiostomatales*. Coloured blocks marked numerically indicate lineages containing *Sporothrix* spp. or *Ophiostoma* spp. with sporothrix-like anamorphs not forming part of any well-defined genus. T indicates ex-type isolates. Significant support values for branches are indicated by bold lines in shades of grey.

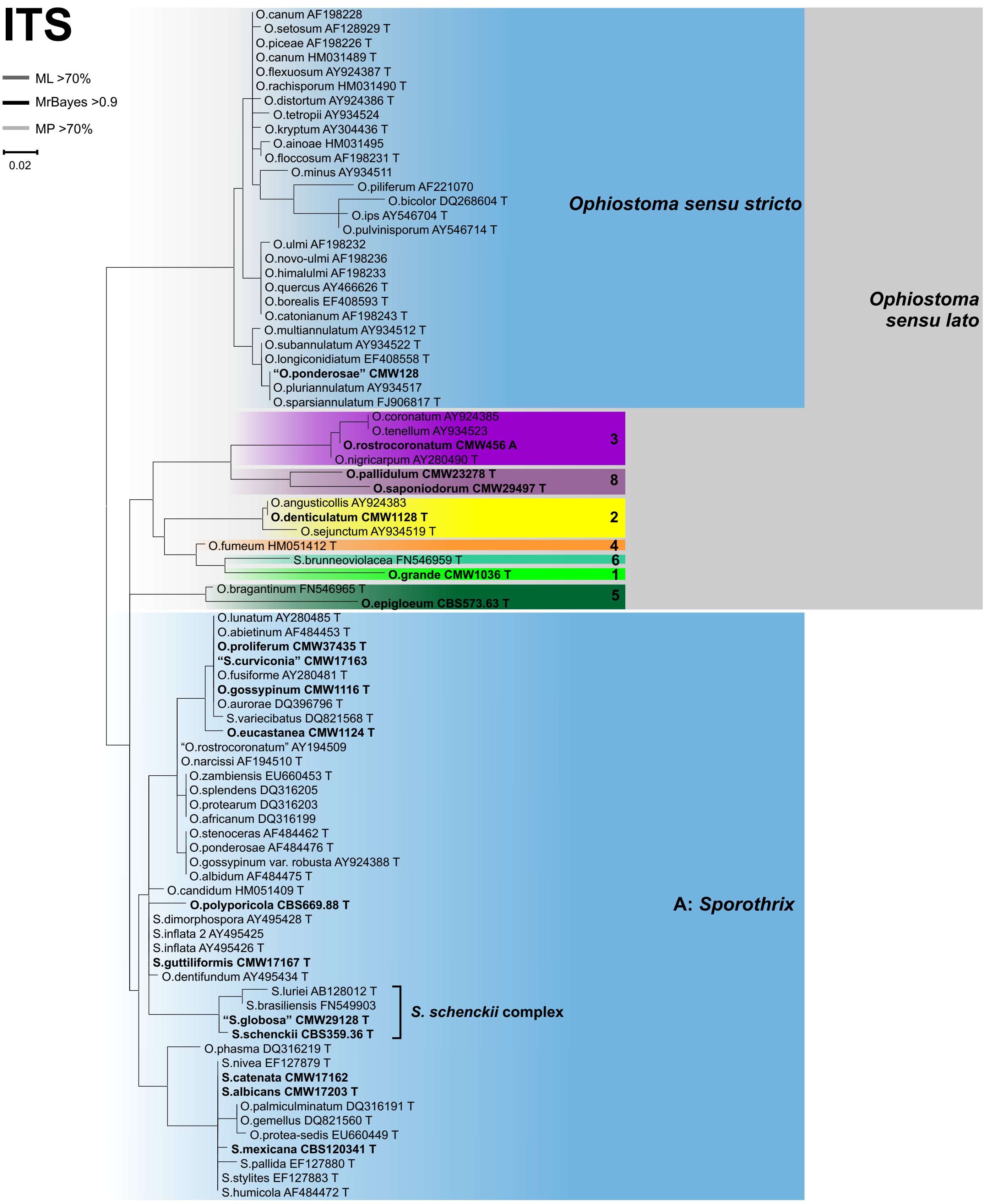
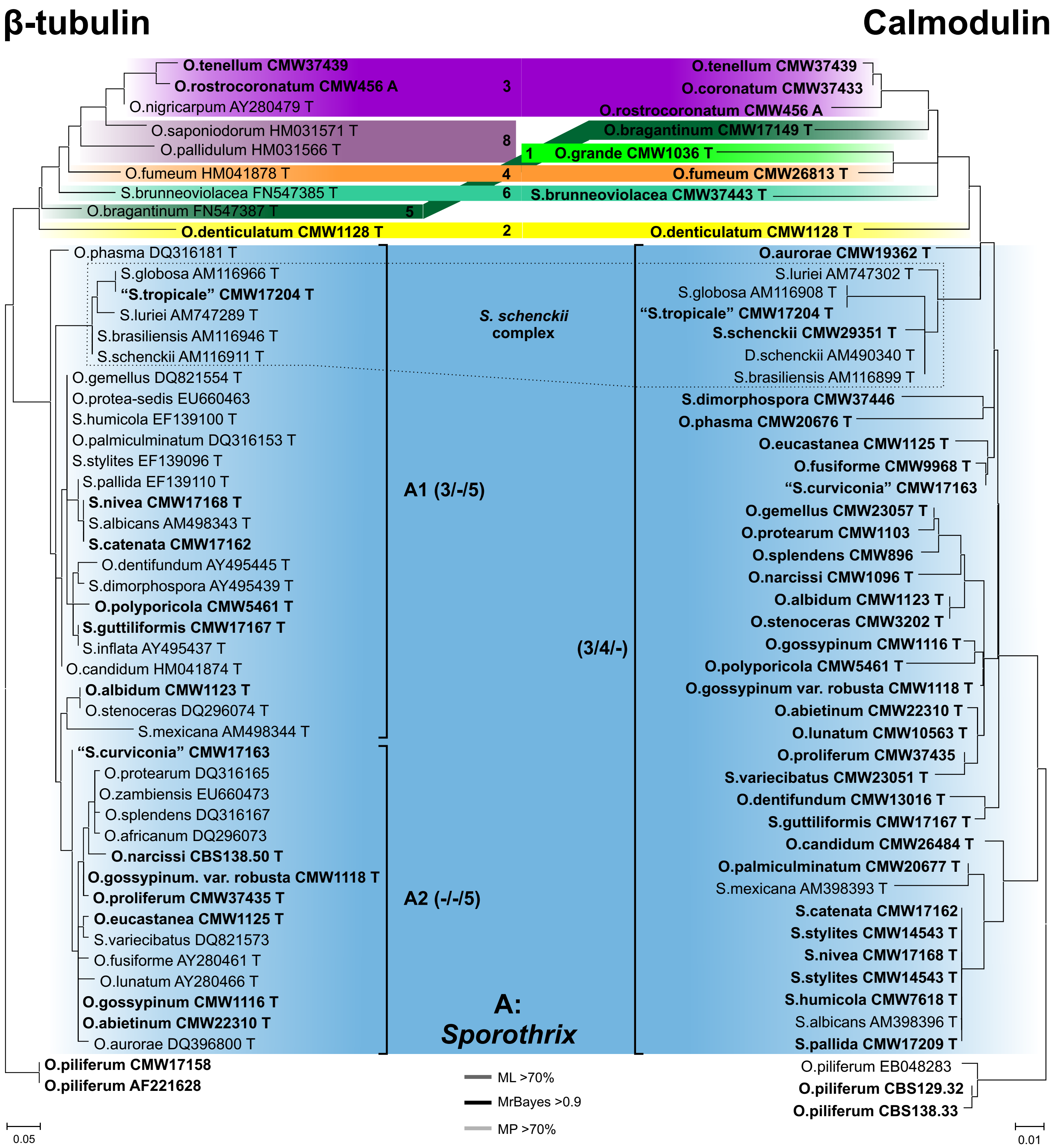

ITS
ML >70%
MrBayes >0.9
MP >70%
0.02
O.canum AF198228
O.setosum AF128929 T
O.piceae AF198226 T
O.canum HM031489 T
O.flexuosum AY924387 T
O.rachisporum HM031490 T
O.distortum AY924386 T
O.tetropii AY934524
O.kryptum AY304436 T
O.ainoae HM031495
O.floccosum AF198231 T
O.minus AY934511
O.piliferum AF221070
O.bicolor DQ268604 T
O.ips AY546704 T
O.pulvinisporum AY546714 T
O.ulmi AF198232
O.novo-ulmi AF198236
O.himalulmi AF198233
O.quercus AY466626 T
O.borealis EF408593 T
O.catonianum AF198243 T
O.multiannulatum AY934512 T
O.subannulatum AY934522 T
O.longiconidiatum EF408558 T
"O.ponderosae" CMW128
O.pluriannulatum AY934517
O.sparsiannulatum FJ906817 T
Ophiostoma sensu stricto
Ophiostoma sensu lato
O.coronatum AY924385
O.tenellum AY934523
O.rostrocoronatum CMW456 A
O.nigricarpum AY280490 T
3
O.pallidulum CMW23278 T
O.saponiodorum CMW29497 T
8
O.angusticollis AY924383
O.denticulatum CMW1128 T
O.sejunctum AY934519 T
2
O.fumeum HM051412 T
4
S.brunneoviolacea FN546959 T
6
O.grande CMW1036 T
1
O.bragantinum FN546965 T
O.epigloeum CBS573.63 T
5
O.lunatum AY280485 T
O.abietinum AF484453 T
O.proliferum CMW37435 T
"S.curviconia" CMW17163
O.fusiforme AY280481 T
O.gossypinum CMW1116 T
O.aurorae DQ396796 T
S.variecibatus DQ821568 T
O.eucastanea CMW1124 T
"O.rostrocoronatum" AY194509
O.narcissi AF194510 T
O.zambiensis EU660453 T
O.splendens DQ316205
O.protearum DQ316203
O.africanum DQ316199
O.stenoceras AF484462 T
O.ponderosae AF484476 T
O.gossypinum var. robusta AY924388 T
O.albidum AF484475 T
O.candidum HM051409 T
O.polyporicola CBS669.88 T
A: Sporothrix
S.dimorphospora AY495428 T
S.inflata 2 AY495425
S.inflata AY495426 T
S.guttiliformis CMW17167 T
O.dentifundum AY495434 T
S.luriei AB128012 T
S.brasiliensis FN549903
"S.globosa" CMW29128 T
S.schenckii CBS359.36 T
S. schenckii complex
O.phasma DQ316219 T
S.nivea EF127879 T
S.catenata CMW17162
S.albicans CMW17203 T
O.palmiculminatum DQ316191 T
O.gemellus DQ821560 T
O.protea-sedis EU660449 T
S.mexicana CBS120341 T
S.pallida EF127880 T
S.stylites EF127883 T
S.humicola AF484472 T

Fig. 3 Phylograms resulting from ML analyses of the BT and CAL exon sequences of *Sporothrix s.str.* and related species in the *Ophiostomatales* with sporothrix-like anamorphs. Intron arrangements are indicated where the number refers to the intron number and – is indicative of a lacking intron. Coloured blocks marked numerically indicate lineages containing *Sporothrix* spp. or *Ophiostoma* spp. with sporothrix-like anamorphs not forming part of any well-defined genus. T indicates ex-type isolates. Significant support values for branches are indicated by bold lines in shades of grey.


β-tubulin
Calmodulin
O.tenellum CMW37439
O.rostrocoronatum CMW456 A
O.nigricarpum AY280479 T
3
O.saponiodorum HM031571 T
O.pallidulum HM031566 T
8
O.fumeum HM041878 T
4
S.brunneoviolacea FN547385 T
6
O.bragantinum FN547387 T
5
O.denticulatum CMW1128 T
2
O.tenellum CMW37439
O.coronatum CMW37433
O.rostrocoronatum CMW456 A
O.bragantinum CMW17149 T
1
O.grande CMW1036 T
O.fumeum CMW26813 T
S.brunneoviolacea CMW37443 T
O.denticulatum CMW1128 T
O.phasma DQ316181 T
S.globosa AM116966 T
"S.tropicale" CMW17204 T
S.luriei AM747289 T
S.brasiliensis AM116946 T
S.schenckii AM116911 T
O.gemellus DQ821554 T
O.protea-sedis EU660463
S.humicola EF139100 T
O.palmiculminatum DQ316153 T
S.stylites EF139096 T
S.pallida EF139110 T
S.nivea CMW17168 T
S.albicans AM498343 T
S.catenata CMW17162
O.dentifundum AY495445 T
S.dimorphospora AY495439 T
O.polyporicola CMW5461 T
S.guttiliformis CMW17167 T
S.inflata AY495437 T
O.candidum HM041874 T
O.albidum CMW1123 T
O.stenoceras DQ296074 T
S.mexicana AM498344 T
"S.curviconia" CMW17163
O.protearum DQ316165
O.zambiensis EU660473
O.splendens DQ316167
O.africanum DQ296073
O.narcissi CBS138.50 T
O.gossypinum. var. robusta CMW1118 T
O.proliferum CMW37435 T
O.eucastanea CMW1125 T
S.variecibatus DQ821573
O.fusiforme AY280461 T
O.lunatum AY280466 T
O.gossypinum CMW1116 T
O.abietinum CMW22310 T
O.aurorae DQ396800 T
O.piliferum CMW17158
O.piliferum AF221628
S. schenckii complex
A1 (3/-/5)
A2 (-/-/5)
(3/4/-)
A: Sporothrix
O.aurorae CMW19362 T
S.luriei AM747302 T
S.globosa AM116908 T
"S.tropicale" CMW17204 T
S.schenckii CMW29351 T
D.schenckii AM490340 T
S.brasiliensis AM116899 T
S.dimorphospora CMW37446
O.phasma CMW20676 T
O.eucastanea CMW1125 T
O.fusiforme CMW9968 T
"S.curviconia" CMW17163
O.gemellus CMW23057 T
O.protearum CMW1103
O.splendens CMW896
O.narcissi CMW1096 T
O.albidum CMW1123 T
O.stenoceras CMW3202 T
O.gossypinum CMW1116 T
O.polyporicola CMW5461 T
O.gossypinum var. robusta CMW1118 T
O.abietinum CMW22310 T
O.lunatum CMW10563 T
O.proliferum CMW37435
S.variecibatus CMW23051 T
O.dentifundum CMW13016 T
S.guttiliformis CMW17167 T
O.candidum CMW26484 T
O.palmiculminatum CMW20677 T
S.mexicana AM398393 T
S.catenata CMW17162
S.stylites CMW14543 T
S.nivea CMW17168 T
S.stylites CMW14543 T
S.humicola CMW7618 T
S.albicans AM398396 T
S.pallida CMW17209 T
O.piliferum EB048283
O.piliferum CBS129.32
O.piliferum CBS138.33
ML >70%
MrBayes >0.9
MP >70%
0.05
0.01

Chapter 5

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Phylogeny of the *Quambalariaceae* fam. nov., including important *Eucalyptus* pathogens in South Africa and Australia

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Abstract: The genus *Quambalaria* consists of plant-pathogenic fungi causing disease on leaves and shoots of species of *Eucalyptus* and its close relative, *Corymbia*. The phylogenetic relationship of *Quambalaria* spp., previously classified in genera such as *Sporothrix* and *Ramularia*, has never been addressed. It has, however, been suggested that they belong to the basidiomycete orders *Exobasidiales* or *Ustilaginales*. The aim of this study was thus to consider the ordinal relationships of *Q. eucalypti* and *Q. pitereka* using ribosomal LSU sequences. Sequence data from the ITS nrDNA were used to determine the phylogenetic relationship of the two *Quambalaria* species together with *Fugomyces* (= *Cerinosterus*) *cyanescens.* In addition to sequence data, the ultrastructure of the septal pores of the species in question was compared. From the LSU sequence data it was concluded that *Quambalaria* spp. and *F. cyanescens* form a monophyletic clade in the *Microstromatales,* an order of the *Ustilaginomycetes*. Sequences from the ITS region confirmed that *Q. pitereka* and *Q. eucalypti* are distinct species. The ex-type isolate of *F. cyanescens*, together with another isolate from *Eucalyptus* in Australia, constitute a third species of *Quambalaria*, *Q. cyanescens* (de Hoog & G.A. de Vries) Z.W. de Beer, Begerow & R. Bauer comb. nov. Transmission electron-microscopic studies of the septal pores confirm that all three *Quambalaria* spp. have dolipores with swollen lips, which differ from other members of the *Microstromatales* (i.e. the *Microstromataceae* and *Volvocisporiaceae*) that have simple pores with more or less rounded pore lips. Based on their unique ultrastructural features and the monophyly of the three *Quambalaria* spp. in the *Microstromatales*, a new family, *Quambalariaceae* Z.W. de Beer, Begerow & R. Bauer fam. nov., is described.

Taxonomic novelties: *Quambalariaceae* Z.W. de Beer, Begerow & R. Bauer fam. nov., *Quambalaria cyanescens* (de Hoog & G.A. de Vries) Z.W. de Beer, Begerow & R. Bauer comb. nov.
Key words: *Cerinosterus, Fugomyces,* ITS, LSU, *Microstromatales, Sporothrix, Ramularia,* ultrastructure, *Ustilaginomycetes*.

INTRODUCTION

During the 1950's, a shoot disease was observed on *Corymbia maculata* (then *Eucalyptus maculata*) seedlings in New South Wales, Australia. The causal fungus was later described as *Ramularia pitereka* J. Walker & Bertus (Walker & Bertus 1971). In 1987, a similar disease was noted on a *Eucalyptus grandis* clone in South Africa. Wingfield *et al.* (1993) described the South African fungus as a new species, *Sporothrix eucalypti* M.J. Wingf., Crous & Swart. In his monograph of *Ramularia* Unger, Braun (1998) transferred *R. pitereka* to *Sporothrix* Hektoen & C.F. Perkins. In the same volume, a third *Sporothrix* species, *S. pusilla* U. Braun & Crous, isolated from leaf spots on *Eucalyptus camaldulensis* in Thailand, was described. Braun (1998) distinguished the three species based on morphology and host specificity. The treatment of the three species in *Sporothrix* (*Ophiostomataceae, Ophiostomatales*), and not *Ramularia* (*Mycosphaerellaceae, Mycosphaerellales*), was based largely on conidial scar morphology (Braun 1998).

Studies prior to Braun's (1998) treatment of the *Eucalyptus* pathogens as species of *Sporothrix* had shown that this genus accommodates superficially similar species with diverse phylogenetic relationships (Weijman & De Hoog 1985, De Hoog 1993). The type species for the genus *Sporothrix*, *S. schenckii* Hekt. & C.F. Perkins, was placed in the teleomorph genus *Ophiostoma* Syd. & P. Syd., based on 18S rDNA sequences (Berbee & Taylor 1992). More recently, Simpson (2000) showed that isolates of *R. pitereka* are not cycloheximide-tolerant, as is almost always the case with *Sporothrix* isolates with affinities to *Ophiostoma* (Harrington 1981). Based on the cycloheximide intolerance, pathogenicity to species of *Eucalyptus* and *Corymbia*, the dense growth of white conidiophores on agar media and the host, and the absence of distinct denticles on the conidiogenous cells, Simpson (2000) concluded that the affinities of *R. pitereka* and the two related species, *S. eucalypti* and *S. pusilla*, are not with the *Ophiostomataceae*. He consequently erected the new genus, *Quambalaria* J.A. Simpson, to accommodate the three species. Simpson (2000), like Braun (1998), distinguished the species based on conidial morphology and specificity to their respective *Eucalyptus* or *Corymbia* hosts. Furthermore, based on the apparent absence of dolipore septa in their hyphae observed by light microscopy, he suggested that these fungi probably reside in either one of the basidiomycete orders *Exobasidiales* Henn., emend. R. Bauer & Oberw., or *Ustilaginales* G. Winter, emend. R. Bauer & Oberw. (Simpson 2000).

There had been one other *Sporothrix*-like fungus isolated from *Eucalyptus pauciflora* in Australia by V.F. Brown. This isolate was sent to CBS in 1973 and was identified as *Sporothrix cyanescens* de Hoog & G.A. de Vries, earlier described from human skin (De Hoog & De Vries 1973). Smith & Batenburg-Van der Vegte (1985) confirmed that *S. cyanescens,* and also *S. luteoalba* de Hoog, have dolipores in their septa and are thus the anamorphs of basidiomycetes. Based on this fact and the presence of the basidiomycetous coenzyme Q-10 system (Suzuki & Nakase 1986), Moore (1987) erected a new genus, *Cerinosterus* R.T. Moore, for the two *Sporothrix* spp., with *C. luteoalbus* (de Hoog) R.T. Moore as generic type species. The first phylogenetic study that included the two *Cerinosterus* spp. showed that *C. luteoalbus* groups within the *Dacrymycetales* Henn. based on LSU sequences (Middelhoven *et al.* 2000). However, *C. cyanescens* (de Hoog & G.A. de Vries) R.T. Moore grouped in the *Microstromatales* R. Bauer & Oberw., and it was suggested that it could not be accommodated in *Cerinosterus*. Sigler & Verweij (2003) thus described a new genus, *Fugomyces* Sigler, with *F. cyanescens* (de Hoog & G.A. de Vries) Sigler as type species.

The aim of this study was to determine whether *Quambalaria* spp. are monophyletic and what their relationship was to *F. cyanescens,* using ITS sequences. Furthermore, ribosomal LSU sequences and ultrastructural characters were used to determine an appropriate order in which species of *Quambalaria* should reside.

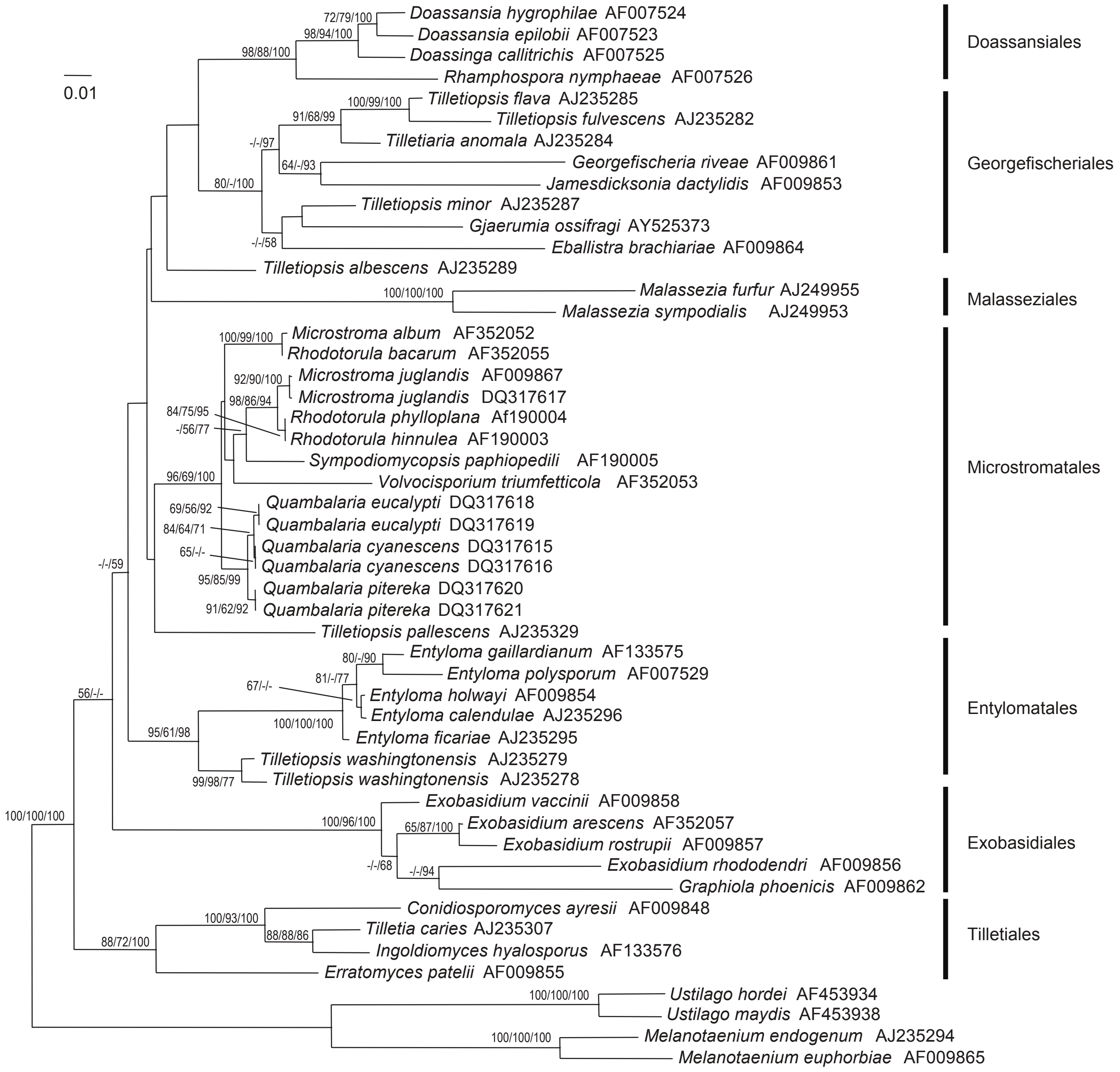


Fig. 1. Phylogram obtained by neighbour-joining analysis using GTR+I+G substitution model of the nuclear LSU region sequences of species in the *Microstromatales*. The topology was rooted with four members of the *Ustilaginomycetidae*. The numbers from left to right refer to percentage bootstrap values of 1000 replicates of neighbour-joining, maximum parsimony, and to *a posteriori* probabilities of Bayesian Markov chain Monte Carlo analysis. Values smaller than 50 % are not shown. Branch lengths are scaled in terms of expected numbers of nucleotide substitutions per site.

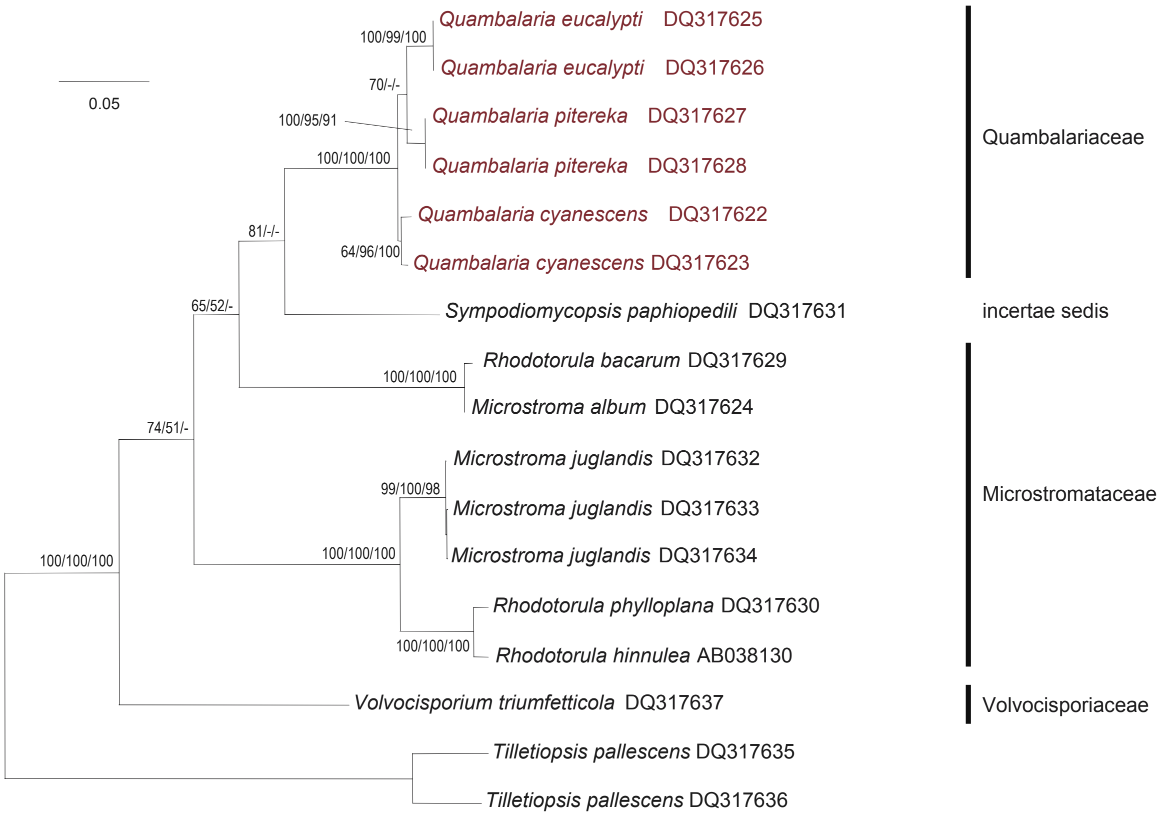


Fig. 2. Phylogram obtained by neighbour-joining analysis of DNA sequences of the nuclear ITS region of species in the *Microstromatales,* using the TVM+I+G substitution model. The topology was rooted with two isolates of *Tilletiopsis pallescens*. The numbers refer to percentage bootstrap values of 1000 replicates of neighbour-joining and maximum parsimony, and to *a posteriori* probabilities of Bayesian Markov chain Monte Carlo analysis. Values smaller than 50 % are not shown. Branch lengths are scaled in terms of expected numbers of nucleotide substitutions per site.

MATERIALS & METHODS

Isolates and herbarium specimens

For phylogenetic studies, two South African isolates of *Q. eucalypti* (M.J. Wingf., Crous & W.J. Swart) J.A. Simpson, including the ex-type culture (CMW 1101 = CBS 118844), were compared with two isolates representing *Q. pitereka* (J. Walker & Bertus) J.A. Simpson from recent disease outbreaks in Queensland, Australia (Table 1). Two isolates representing *F. cyanescens,* including the ex-type culture (CBS 357.73), were also included. Other isolates for which DNA sequences were obtained in this study, are listed in Table 1. GenBank accession numbers of sequences obtained in previous studies, are indicated in Figs 1–2.

For ultrastructural examinations of *Q. pitereka* and *Q. eucalypti*, herbarium specimens of naturally infected leaves and stems were used (Table 1). These specimens had been deposited in the National Collection of Fungal Specimens, Pretoria, South Africa (PREM). The holotype of *Q. eucalypti* (PREM 51089) consists of a dried culture on 2 % MEA. However, some important morphological and ultrastructural characters are only expressed on host tissue. The *Q. eucalypti* specimen we used for ultrastructural work (PREM 58939), consists of symptomatic leaf tissue, collected from the same host in the same location as the holotype (Table 1). This material is designated here as epitype for *Q. eucalypti*. The culture associated with the epitype (CBS 119680 = CMW 11678), was also included in the phylogenetic analyses. Specimen or isolate numbers of other species in the *Microstromatales* used for ultrastructural work, are underlined in Table 1.

The ex-type culture of *Q. pusilla* (U. Braun & Crous) J.A. Simpson (CMW 8279) was found to be contaminated with a *Verticillium* species and could not be purified. Attempts to extract DNA from the holotype specimen (HAL) were not successful. This species was therefore not included in the study.

DNA extraction and PCR

For the phylogenetic analyses, isolates were grown for 7 d on 2 % malt extract agar. DNA extraction, PCR conditions, visualization and purification of PCR products, as well as DNA sequencing, were done as described by Aghayeva *et al.* (2004). The internal transcribed spacer region (ITS1, the 5.8S rRNA gene and ITS2), was amplified using PCR with the primers ITS1 and ITS4 (White *et al.* 1990). The 5' end of the ribosomal large subunit (LSU) was amplified using primers NL1 and NL4 (O'Donnell 1993).

Phylogenetic analyses

Both alignments were assembled with MAFFT 3.85 (Katoh *et al.* 2002) using the accurate and iterative refinement method (FFT-NS-i settings). After trimming of both ends, the LSU alignment consisted of 572 bp and the ITS alignment of 726 bp. Phylogenetic analyses were carried out using PAUP v. 4.0b10 (Swofford 2001).

Table 1. Isolates and herbarium specimens used in this study.

Species	CBS numbers	Isolate number	Herbarium number	Host	Origin	Collector	GenBank	
							ITS	LSU
Microstroma album			R.B. 2072	*Quercus robur*	Germany	R. Bauer	DQ317624	AF352052
M. juglandis		F3381		*Juglans regia*	Germany	M. Göker	DQ317632	–
			R.B. 2054	*J. regia*	Germany	R. Bauer	DQ317633	–
			R.B. 2042	*J. regia*	Germany	R. Bauer	DQ317634	DQ317617
Quambalaria cyanescens = *Fugomyces cyanescens*	CBS 357.73^{1T}	CMW 5583		skin of man	Netherlands	T.F. Visser	DQ317622	DQ317615
	CBS 876.73	CMW 5584		*Eucalyptus pauciflora*	New South Wales, Australia	V.F. Brown	DQ317623	DQ317616
Q. eucalypti	CBS 118844^{T}	CMW 1101	PREM 51089^{T}	*E. grandis*	Kwambonambi, South Africa	M.J. Wingfield	DQ317625	DQ317618
	CBS 119680	CMW 11678	PREM 58939^{E}	*E. grandis* clone NH58	Kwambonambi, South Africa	L. Lombard	DQ317626	DQ317619
Q. pitereka		CMW 6707		*Corymbia maculata*	New South Wales, Australia	M.J. Wingfield	DQ317627	DQ317620
	CBS 118828	CMW 5318		*C. citriodora* subsp. *variegata*	Queensland, Australia	M. Ivory	DQ317628	DQ317621
			PREM 58940	*C. citriodora* subsp. *variegata*	Queensland, Australia	G.S. Pegg	–	–
Rhodutorula bacarum	CBS 6526^{T}	IGC4391		*Ribes nigrum*	United Kingdom	R.W.M. Buhagiar	DQ317629	AF352055
R. hinnulea	CBS 8079^{T}	IGC4849		*Banksia collina*	Australia	R.G. Shivas	AB038130	AF190003
R. phylloplana	CBS 8073^{T}	IGC4246		*B. collina*	Australia	R.G. Shivas	DQ317630	AF190004
Sympodiomycopsis paphiopedili	CBS 7429^{T}	IGC5543		nectar of *Paphiopedilum primurinum*	Japan	K. Tokuoka	DQ317631	AF190005
Tilletiopsis pallescens		F3370		fern leaf	Germany	J.P. Sampaio	DQ317635	–
	CBS 606.83^{T}	ATCC24345		basidiome of *Sirobasidium* sp.	Japan	R.J. Bandoni	DQ317636	–
Volvocisporium triumfetticola			R.B. 2070^{T}	*Triumfetta rhomboidea*	India	M.S. Patil	DQ317637	AF352053

[1] Underlined culture collection or herbarium numbers indicate isolates or specimens used in TEM studies.

[T] Holotype specimens or ex-type isolates.

[E] Epitype; CBS = Centraalburaeu voor Schimmelcultures, Utrecht, The Netherlands; CMW = Culture Collection of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa; R.B. = Herbarium R. Bauer, Tübingen, Germany; F = Culture Collection, Tübingen, Germany; PREM = National Collection of Fungal Specimens, Pretoria, South Africa; IGC = Portugese Yeast Culture Collection, Portugal; ATCC = American Type Culture Collection, Manassas, Virginia, U.S.A.

Table 2. Higher classification and definitions of families in the *Microstromatales*. Extracted from Bauer *et al*. (1997), Begerow *et al*. (2001), and the results of this study.

Ustilaginomycetes			
phytoparasitic members of the Basidiomycota lacking dolipores with multilayered pore caps interactions with deposits of specific fungal vesicles			
Exobasidiomycetidae			
local interaction zones septa having pores with membranous caps or septa poreless at maturity			
Microstromatales			
no interaction apparatus no teliospores			
Microstromataceae	***Volvocisporiaceae***	***Quambalariaceae***	**incertae sedis**
aseptate basidiospores	septate basidiospores	sexual state unclear	sexual state not observed
simple pores with more or less rounded pore lips		dolipores with swollen pore lips	no pores, septa occasionally with median swellings
septal pores enclosed on both sides by membrane caps			
Teleomorphic genera & species			
Microstroma	***Volvocisporium***		
basidia protrude through stomata & sporulate in gasteroid mode of spore release on leaf surface	septate basidiospores with peripheral layer of cells	teleomorph unclear or not observed	
> 37 species	*V. triumfetticola*		
Anamorphic genera & species			
Rhodotorula		***Quambalaria***	***Sympodiomycopsis***
R. bacarum *R. phylloplana* *R. hinnulea*		*Q. pitereka* *Q. eucalypti* *Q. cyanescens* *Q. pusilla?*	*S. paphiopedili*

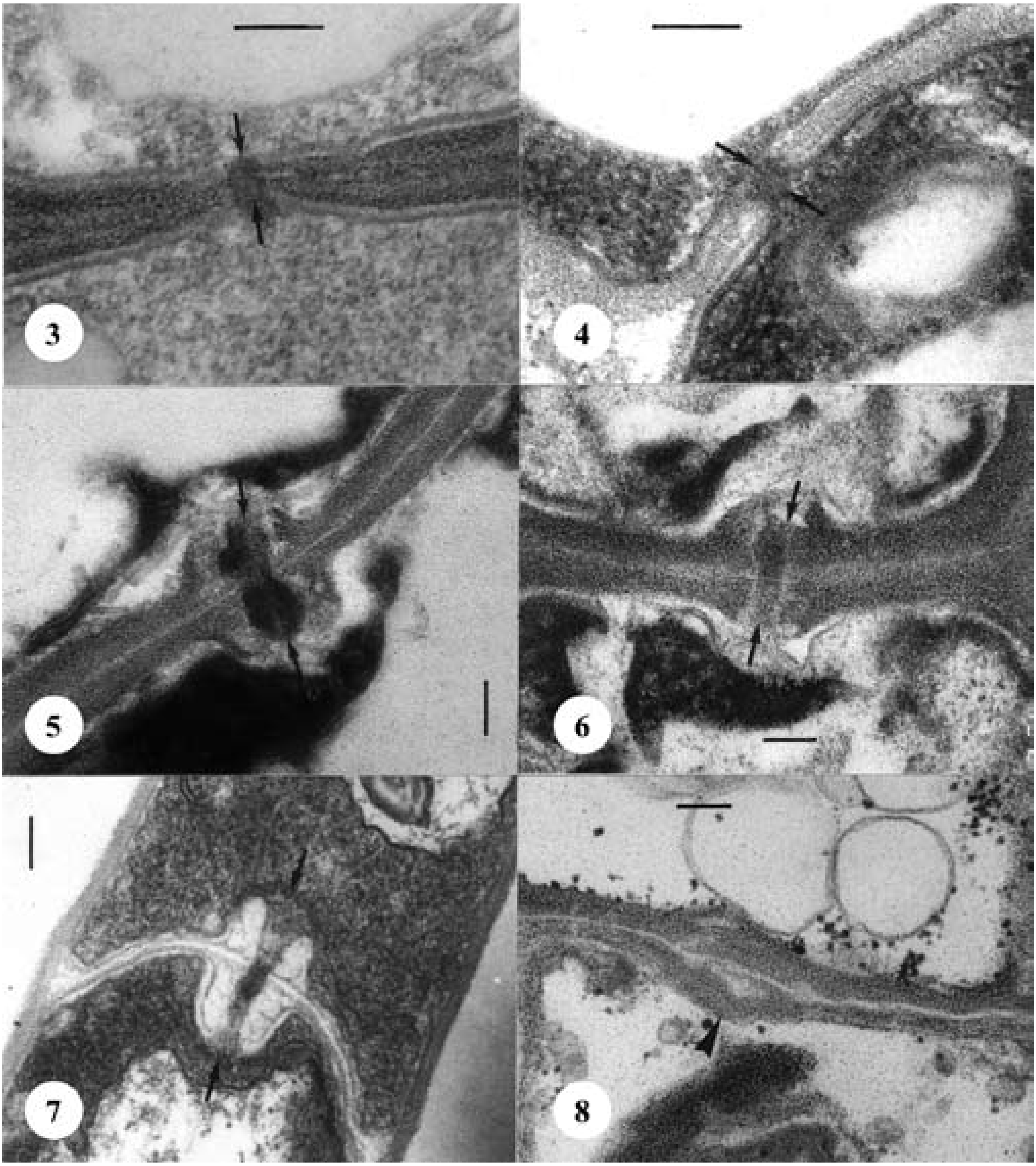
Modeltest 3.0 (Posada & Crandall 1998) was applied to determine a model of DNA substitution that fits the data set. GTR+I+G was selected from the Akaike information criterion for the LSU alignment (base frequencies: $\pi_A = 0.2563$, $\pi_C = 0.1950$, $\pi_G = 0.2911$, $\pi_T = 0.2576$; substitution rates: A/C = 0.7670, A/G = 2.6760, A/T = 0.7823, C/G = 0.3153, C/T = 5.9744, G/T = 1.0000; gamma shape parameter = 0.7950; percentage of invariant sites = 0.3790). TVM+I+G was selected from the Akaike information criterion for the ITS alignment (base frequencies: $\pi_A = 0.2535$, $\pi_C = 0.2188$, $\pi_G = 0.2157$, $\pi_T = 0.3120$; substitution rates: A/C = 0.14911, A/G C/T = 5.2884, A/T = 2.1848, C/G = 0.8252, G/T = 1.0000; gamma shape parameter = 1.6440; percentage of invariant sites = 0.3892). Neighbour-joining analysis was done determining genetic distances according to the specified substitution model.

Parsimony analysis was conducted in two steps where the first with 10.000 random additions without branch swapping resulted in two islands for the LSU alignment and six for the ITS alignment. Subsequent TBR swapping over the best trees of these islands resulted in four most parsimonious trees for the LSU alignment with 1025 steps (CI = 0.404; RI = 0.665; RC = 0.269), and six trees for the ITS alignment with 507 steps (CI = 0.789; RI = 0.857; RC = 0.676), using 1000 replicates for bootstrap analyses.

For Bayesian analysis, four incrementally heated simultaneous MCMC Markov chains were run over 1 000 000 generations using the general time-reversible model (six rate classes) including a proportion of invariant sites and gamma-distributed substitution rates of the remaining sites (GTR+I+G) (for description of models see Swofford *et al.* 1996). Trees were sampled every 100th generation, resulting in an overall sampling of 10 000 trees. From these, the first 3000 trees were discarded (as burn-in). MrBayes 3.0b3 (Huelsenbeck & Ronquist 2001) was used to compute a 50 % majority rule consensus of the remaining trees to obtain estimates for the posterior probabilities.

Transmission Electron Microscopy

Species representing the major groups in the *Microstromatales*, were selected for ultrastructural studies (Table 1). For transmission electron microscopy (TEM), samples were fixed overnight with 2 % glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.2) at 20 °C. Following six transfers in 0.1M sodium cacodylate buffer, samples were postfixed in 1 % osmium tetroxide in the same buffer for 1 h in the dark, washed in bidistilled water, and stained with 1 % aqueous uranyl acetate for 1 h in the dark. After five consecutive washes in bidistilled water, samples were dehydrated in acetone, using 10 min transfers at 10, 25, 50, 70, 95, and three times in 100 % acetone. Samples were embedded afterwards in Spurr´s plastic and sectioned with a diamond knife. Ultra-thin serial sections were mounted on formvar-coated, single-slot copper grids, stained with lead citrate at room temperature for 5 min, and finally washed with bidistilled water. The samples were studied using a Zeiss EM 109 transmission electron microscope operating at 80 kV.



Figs 3–8. Septation in the *Microstromatales*. 3. Simple pore with two membrane caps (arrows) of *Microstroma juglandis*. 4. Simple pore with two membrane caps (arrows) of *Volvocisporium triumfetticola*. 5. Dolipore of *Quambalaria eucalypti* with two membrane caps (arrows) from herbarium material. 6. Dolipore with two membrane caps (arrows) of *Quambalaria pitereka* from herbarium material. 7. Dolipore with two membrane caps (arrows) of *Fugomyces cyanescens* (CBS 357.73). 8. Pore equivalent in *Sympodiomycopsis paphiopedili* (CBS 7429). Septum with median swelling (arrowhead), but without cytoplasmic continuim between adjacent cells. Scale bars = 0.1 µm.

RESULTS

Phylogenetic analyses

The different phylogenetic analyses of the LSU dataset resulted in similar topologies resolving all known orders of *Exobasidiomycetidae* Jülich, emend. R. Bauer & Oberw. (Fig. 1). The *Tilletiales* H. Kreisel *ex* R. Bauer & Oberw. were weakly supported as sistergroup to the other orders. Although the backbone was not resolved in all parts, the specimens of *Quambalaria* and *Fugomyces* considered in this study clustered within the *Microstromatales* as a highly supported monophylum in both datasets. *Tilletiopsis pallescens* Gokhale clustered together with members of the *Microstromatales* and it was, therefore, used as outgroup for the ITS dataset of the *Microstromatales*.

The ITS regions were used to elucidate the inner phylogeny of the *Microstromatales* (Fig. 2). *Volvocisporium triumfetticola* (Patil) Begerow, R. Bauer & Oberw., the only known member of the *Volvocisporiaceae* Begerow, R. Bauer & Oberw., was sister to the other members of the *Microstromatales*. *Microstroma* Niessl appeared paraphyletic in the LSU and ITS analyses, and the relationship between the two *Microstroma* clusters was weakly supported. This could have resulted from the unclear positions of *Sympodiomycopsis paphiopedili* Sugiy., Tokuoka & Komag. and *V. triumfetticola*. All studied specimens of *Quambalaria* and *Fugomyces* appeared to form a monophylum. The monophyly of *Quambalaria eucalypti* and *Q. pitereka* was supported only in the ITS neighbour-joining analysis and was rejected by maximum parsimony and Bayesian inference and by the LSU data. *Quambalaria eucalypti*, *Q. pitereka* and the *Fugomyces* isolates formed three separate, well-supported clusters. Sequences of the two *Q. eucalypti* isolates (ex-type and ex-epitype cultures) were identical, and also those of the two *Q. pitereka* isolates. The ITS sequences of two *F. cyanescens* isolates differed from each other by 4 bp.

Transmission Electron Microscopy

Septal pore apparatuses in the studied species of *Microstroma* and *Volvocisporium* Begerow, R. Bauer & Oberw. were simple with more or less rounded pore lips, which were enclosed on both sides by membrane caps (Figs 3–4). In *Quambalaria pitereka*, *Q. eucalypti* and *Fugomyces cyanescens,* the pores were also enclosed by membrane caps, but the septal pore apparatus consisted of dolipores with swollen pore lips (Figs 5–7). In the anamorphic yeast, *Sympodiomycopsis paphiopedili* we found no septal pores. Occasionally, the septa possess median swellings resembling septal pores, but there was no cytoplasmic continuum between adjacent cells (Fig. 8).

TAXONOMY

Phylogenetic analyses of the LSU data obtained in this study showed that the genus *Quambalaria* resides in the *Microstromatales*. However, the ultrastructure of the septal pores of *Quambalaria* spp. differ substantially from those of species in the *Microstromataceae* Jülich and *Volvocisporiaceae*. We, therefore, describe a new family, *Quambalariaceae,* to accommodate the species with dolipores. Thus, the *Microstromatales* now include not only taxa having septa with simple pores, but also taxa with dolipores or septa without pores. Ultrastructural characteristics*,* together with LSU and ITS data, show that *Fugomyces cyanescens* is clearly monophyletic with the two sampled *Quambalaria* spp. *Fugomyces* is therefore synonymised here with *Quambalaria* and the necessary new combination is established.

Quambalariaceae Z.W. de Beer, Begerow & R. Bauer, **fam. nov.** MycoBank MB500889.

Socii Microstromatalium doliporos cum labiis pororum tumidis facientes.

Members of the *Microstromatales* having dolipores with swollen pore lips.

Quambalaria J.A. Simpson, Australas. Mycol. 19: 60–61. 2000.

= *Fugomyces* Sigler, *Manual of clinical microbiology, Vol. 2*: 1753. 2003.

(1) Type species: ***Quambalaria pitereka*** (J. Walker & Bertus) J.A. Simpson, Australas. Mycol. 19: 60. 2000.

Basionym: *Ramularia pitereka* J. Walker & Bertus, Proc. Linn. Soc. New South Wales 96(2): 108. 1971.

≡ *Sporothrix pitereka* (J. Walker & Bertus) U. Braun & Crous, In Braun, *A monograph of Ramularia, Cercosporella and allied genera (phytopathogenic hyphomycetes)*: 416. 1998.

Specimens examined: **Australia**, Queensland, *Corymbia citriodora* subsp. *variegata* leaves, 09 June 1999, M. Ivory, CBS 118828 = CMW 5318; *C. citriodora* subsp. *variegata* leaves, 2002, G.S. Pegg, PREM 58940; New South Wales, Grafton, *C. maculata* leaves, Dec. 2000, M.J. Wingfield, CMW 6707.

(2) ***Quambalaria cyanescens*** (de Hoog & G.A. de Vries) Z.W. de Beer, Begerow & R. Bauer, **comb. nov.** MycoBank MB500890.

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

≡ *Cerinosterus cyanescens* (de Hoog & G.A. de Vries) R.T. Moore, Stud. Mycol. 30: 216. 1987.

≡ *Fugomyces cyanescens* (de Hoog & G.A. de Vries) Sigler, In Murray, *Manual of clinical microbiology, Vol. 2*: 1753. 2003.

Specimens examined: **Australia**, New South Wales, Armidale, *Eucalyptus pauciflora*, 1973, V.F. Brown, CBS 876.73 = CMW 5584. **Netherlands**, Groningen, skin of man, 18 Oct 1959, T.F. Visser, **holotype** culture ex-type CBS 357.73 = CMW 5583.

(3) ***Quambalaria eucalypti*** (M.J. Wingf., Crous & W.J. Swart) J.A. Simpson, Australas. Mycol. 19: 61. 2000.

Basionym: *Sporothrix eucalypti* M.J. Wingf., Crous & W.J. Swart, Mycopathologia 123: 160. 1993.

Specimens examined: **South Africa**, KwaZulu-Natal, Kwambonambi, *Eucalyptus grandis* leaves, 19 May 1987, M.J. Wingfield, holotype PREM 51089; KwaZulu-Natal, Kwambonambi, *E. grandis* leaves, 2001, L. Lombard, PREM 58939, **epitype designated here**, culture ex-epitype CBS 119680 = CMW 11678.

Species of uncertain status

(a) ***Sporotrichum destructor*** H.A. Pittman, In Cass

Smith, J. Agric. W. Austral. 11 (2): 34. 1970. (*nom. nud.*)

Note: This fungus, resembling other *Quambalaria* spp., was isolated by H.A.J. Pittman in 1935 from diseased *Corymbia ficifolia* in Western Australia. Cultures were sent to Kew where it was identified as a new species named *Sporotrichum destructor* H.A. Pittman (Cass Smith 1970). However, a Latin diagnosis was never published and material of this species was not available for this study.

(b) ***Quambalaria pusilla*** (U. Braun & Crous) J.A. Simpson, Australas. Mycol. 19: 61. 2000.
Basionym: *Sporothrix pusilla* U. Braun & Crous, In Braun, *A monograph of Ramularia, Cercosporella and allied genera (phytopathogenic hyphomycetes)*: 418. 1998.

Note: The ex-type culture of this species (CMW 8279) was contaminated and DNA could not be extracted from the holotype specimen (HAL). The phylogenetic status of this species shall only become clear if fresh material can be obtained.

DISCUSSION

In this study we have produced phylogenetic evidence showing that *Q. pitereka* infecting *Corymbia* spp. in Australia and *Q. eucalypti,* the fungal pathogen on *Eucalyptus grandis* in South Africa, indeed represent two distinct species. Both LSU and ITS sequence data sets revealed that the two *Quambalaria* spp. and *F. cyanescens* (now *Q. cyanescens*) form a monophyletic lineage in the basidiomycete order *Microstromatales*. The monophyly of *Quambalaria* is supported by ultrastructural features. *Quambalaria* differs from other genera in the *Microstromatales* because it has dolipores with swollen pore lips in the septa, and not simple pores with more or less rounded pore lips, which are characteristic of the *Microstromataceae* and *Volvocisporiaceae*. We have thus described a new family, *Quambalariaceae*, in the *Microstromatales* to accommodate *Quambalaria* spp.

Taxa in the *Microstromatales* are classified in the subclass *Exobasidiomycetidae* of the *Ustilaginomycetes* (Table 2). With few exceptions, the *Ustilaginomycetes* are restricted to angiosperms, and most are parasites of monocots (Bauer *et al.* 1997). Of the at least seven orders in the *Ustilaginomycetes* (Fig. 1), members of only two, the *Exobasidiales* and the *Microstromatales,* do not form teliospores and occur on woody bushes or trees (Begerow *et al.* 2001). The *Exobasidiales* differ from the *Microstromatales* by the formation of complex interaction apparatuses including interaction rings (Bauer *et al.* 1997). The *Exobasidiales* represent a large order including at least nine genera in four families (Begerow *et al.* 2002a). The largest of these is *Exobasidium* Woronin with over 100 species occurring world-wide on flowering plants such as the *Ericaceae*. Another well-known genus of the *Exobasiales* is *Graphiola* Poit., which includes more than 12 species, occurring exclusively on *Arecaceae* (palms), also with a global distribution (http://nt.arg-grin.gov/fungaldatabases/fungushost/FungusHost.cfm and http://www.indexfungorum.org). A third genus of this order is *Muribasidiospora* O. Kamat & Rajendren (Begerow *et al.* 2001). *Muribasidiospora indica* O. Kamat & Rajendren was recently reported from South Africa for the first time, causing a prominent leaf spot on native *Rhus lancea* (Crous *et al.* 2003).

The *Microstromatales* are characterised by the lack of teliospores and interaction apparatus (Bauer *et al.* 1997). Only two teleomorphic genera are known in the *Microstromatales* (Table 2). One of these is *Volvocisporium* (Table 2 and Fig. 2) which is monotypic. This fungus has such a unique morphology that it was placed in a family of its own (Begerow *et al.* 2001). The dominant genus in the *Microstromatales* is *Microstroma* including about 35 species occurring world-wide, primarily on *Leguminosae*, *Fagaceae* and *Juglandaceae* (http://nt.arg-grin.gov/fungaldatabases/fungushost/FungusHost.cfm and http://www.indexfungorum.org). Only two *Microstroma* spp. have been reported from South Africa: *M. album* (Desm.) Sacc. from *Quercus*, both exotic, and *M. albiziae* Syd. & P. Syd. from three native *Albizia* spp. (Doidge 1950). Similarly, two exotic *Microstroma* spp. have been reported from Australia: again *M. album* from *Quercus* and, additionally, *M. juglandis* (Berenger) Sacc. from *Juglans* (Sampson & Walker 1982, Shivas 1989). *Microstroma album* (Fig. 2) is known only from *Quercus* and has been reported widely from the Northern hemisphere. *Microstroma juglandis* (Fig. 2) has been found on different genera belonging to the *Juglandaceae*, with a global distribution. *Microstroma albiziae* has only been reported from *Albizia* spp. in South Africa (Doidge 1950) and India (Mathur 1979). Material of these species was not available for study.

Begerow *et al*. (2001) showed with LSU sequence analyses that two anamorphic yeasts, *Rhodotorula bacarum* (Buhagiar) Rodr. Mir. & Weijman and *R. phylloplana* (R.G. Shivas & Rodr. Mir.) Rodr. Mir. & Weijman are phylogenetically closely related to *Microstroma album* and *M. juglandis*, respectively. Our ITS data (Fig. 2), support their results and show that *R. bacarum* might be the same species as *M. album*. We included a third species, *R. hinnulea* (R.G. Shivas & Rodr. Mir.) Rodr. Mir. & Weijman, and it differs from *R. phylloplana* in only 2 bp. (Fig. 2). Both these species were isolated from the leaves of *Banksia collina* (*Proteaceae*) in Australia, and were described then as new *Cryptococcus* species (Shivas & Rodrigues de Miranda 1983). However, the biochemical and morphological differences (Shivas & Rodrigues de Miranda 1983) between the two species are small and they might represent individuals of the same species. The three *Rhodotorula* spp. should not be accommodated in the genus *Rhodotorula*, because the type species for *Rhodotorula*, *R. glutinis* (Fresen.) F.C. Harrison, is phylogenetically (based on sequence data) placed in the *Sporidiales* R.T. Moore in the *Urediniomycetes* (Swann & Taylor 1995). We have chosen not to erect a new anamorph genus for these fungi at the present time, since they might be linked to teleomorphs (probably *Microstroma* spp.) and could be more appropriately treated at a time when additional material is available for study.

The monophyly (Fig. 2) and ultrastructural similarities (Figs 5–7) between the three *Quambalaria* spp. recognised in this study, is supported by the ecology of these species. The fact that all three species, as well as *Q. pusilla* (not included), occur on tree species native to Australia, suggests that Australia is the centre of origin of these species. Although *Q. cyanescens* has been isolated from human tissues on several occasions, the fungus has not been associated with specific disease symptoms of humans (Middelhoven *et al.* 2000, Sigler & Verweij 2003). Inoculation trials on mice failed to demonstrate virulence of the fungus on mammals (Sigler *et al.* 1990). The fungus is, therefore, rather regarded as an opportunist, and potentially can be implicated in disease in immunocompromised patients (Tambini *et al.* 1996).

The recognition of *Quambalaria* spp. as basidiomycetes has not been widely considered because the teleomorph has never been observed. When the teleomorph morphology of the closely related fungus *M. juglandis* is considered (Begerow *et al.* 2001), it might be found that the teleomorph of *Quambalaria* is masquerading as an anamorph. This is entirely possible as the anamorph and teleomorph states would be difficult to distinguish from each other.

One of the species for which the position in the *Microstromatales* remains uncertain (Table 2 and Fig. 2), is the anamorphic yeast *Sympodiomycopsis paphiopedili*. This fungus was described from the nectar of an orchid in Japan (Sugiyama *et al.* 1991). Although the conidiogenous cells in culture (Sugiyama *et al.* 1991) resemble those of *Quambalaria*, its phylogenetic position (Fig. 2) sets it apart from all the other members of the *Microstromatales*. Because this yeast forms pseudomycelia, occasionally with retraction septa, it is not surprising that we did not observe pores (Bauer *et al.* 2001), but septa with median swellings (Fig. 8). Suh *et al.* (1993) reported simple pores in *S. paphiopedili*, but the respective micrograph is insufficient. The pore structure of the hyphal phase of *S. paphiopedili* is thus unknown.

Recognition of three families in the *Microstromatales* and emerging lineages that correspond with host families, follows a trend that has been observed in other orders in the *Ustilaginomycetes* (Begerow *et al.* 2004). The four families in the *Exobasidiales*, for example, can be distinguished based on basidial morphology and host range, but these characteristics also match phylogenetic lineages based on LSU rDNA sequences (Begerow *et al.* 2002a). Cospeciation of groups of species in the *Entylomatales* R. Bauer & Oberw. with their hosts, has also been shown (Begerow *et al.* 2002b). To test cospeciation processes in the *Microstromatales*, additional fungal isolates from a wider variety of hosts would need to be included in phylogenetic studies together with their host species. However, there is good evidence that *Q. pitereka* infects only *Corymbia* and *Q. eucalypti* is restricted to hosts in the genus *Eucalyptus*. These two tree genera are phylogenetically distinct (Hill & Johnson 1995, Wilson *et al.* 2001) and it appears that the pathogens have specifically evolved to infect them.

Studies on members of the *Microstromatales* have been limited, most likely because they have not been considered an economically important group of fungi. This perception is changing rapidly with the reported spread of disease caused by members of the *Quambalariaceae* in commercial *Eucalyptus* plantations in South Africa (Wingfield *et al.* 1993), Brazil and Uruguay (Alfenas *et al.* 2001, Zauza *et al.* 2003), and in *Corymbia* plantations in Australia (Simpson 2000, Pegg *et al.* 2005). That we have only touched the “tip of the iceberg” of the *Microstromatales* (Begerow *et al.* 2001) should be regarded as a challenge, since so many questions surrounding the biology and distribution of this intriguing group of fungi remain unanswered.

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Chapter 6

Quambalaria: new reports from four continents, including *Q. purpurascens* nom. prov. from diseased *Angophora costata* in Australia

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Abstract

The genus *Quambalaria* (*Microstromatales, Ustilaginomycetes*) accommodates six species, all of which are associated with diseases on myrtaceous trees. Five of the species have been defined based on DNA sequences, but for one species, *Q. pusilla* this has not been possible due to the fact that there has not been a living culture available for it. In recent years, 39 *Quambalaria* isolates from various hosts in South Africa, Thailand, Laos, the USA, Tunisia and Australia had become availabe for study. In addition, a dried culture of the ex-type specimen of *Q. pusilla* was discovered, which made DNA analyses for this taxon possible. In this study we characterized all these isolates and the herbarium specimen based on ITS sequences. A second aim was to explore other gene regions that can support ITS data for species level differentiation. Basidiomycete specific primers were developed for the elongation factor 1α (EF) gene based on several publicly available genome sequences including species in the *Ustilaginales*, *Pucciniales*, and *Tremellales*. These primers made it possible to amplify and sequence the EF gene for all the isolates included in the study, as well as several reference isolates. The phylogenies obtained using the EF data corresponded well with those based on ITS data, and revealed six well-supported monophyletic clades representing *Q. pitereka*, *Q. eucalypti*, *Q. cyanescens*, *Q. coyrecup*, *Q. pusilla* (with *Q. simpsonii* as synonym), and a novel taxon from leaf spots on *Angophora costata* in Australia, described here as *Q. purpurascens* nom. prov. Furthermore, the data revealed new host records for *Q. coyrecup, Q. cyanescens* and *Q. pitereka* from *A. costata* New South Wales, and *Q. pitereka* from *Corymbia tessellaris* and *C. ptychocarpa* in Queensland. New country reports from diseased *Eucalyptus* leaves include *Q. eucalypti*, *Q. pusilla* and *Q. cyanescens* from Laos, and *Q. eucalypti* from Thailand. *Quambalaria cyanescens* was the only species to occur on hosts other than those in the *Myrtaceae* as well as on all inhabitable continents, in association with several hardwood-infesting bark beetles from Colorado and California in the USA, and from Tunisia. The fact that Australia is the only country where all six *Quambalaria* spp. have been reported, suggests that this continent is the centre of origin of the genus.

Taxonomic novelties

Quambalaria purpurascens Z.W. de Beer, Marinc. & G.S. Pegg nom. prov.

INTRODUCTION

The genus *Quambalaria* was established by Simpson (2000) to accommodate three species that cause leaf and shoot blight diseases previously treated in *Sporothrix* (Wingfield *et al.* 1993; Braun 1998) and *Ramularia* (Walker & Bertus 1971). The first DNA based treatment of *Quambalaria,* with sequence data for three species, placed the genus in the *Quambalariaceae,* a new family in the *Microstromatales* (*Ustilaginomycetes*) (De Beer *et al.* 2006). The species included in this study were *Q. pitereka* and *Q. eucalypti,* respectively associated with *Corymbia* and *Eucalyptus* leaf diseases, as well as *Q. cyanescens,* an apparently opportunistic human pathogen with a wide host range (**Table 1**). A fourth species, *Q. pusilla*, was placed in *Quambalaria* based on morphology (Simpson 2000), but De Beer *et al.* (2006) found that the ex-type culture had become contaminated and they consequently could not resolve its phylogenetic placement.

Two additional species have subsequently been described in *Quambalaria*. These include *Q. coyrecup* associated with a canker disease of *Corymbia* in Western Australia (Paap *et al.* 2008), and *Q. simpsonii* from leave spots of *Eucalyptus* in Thailand and the Northern Territory of Australia (Cheewangkoon *et al.* 2009). All studies reporting species of *Quambalaria* from new hosts and geographic locations are are listed in **Table 1**, with a visual summary presented in **Fig. 1**.

In recent years, several isolates of *Quambalaria*-like fungi have been obtained from a variety of hosts and geographic locations. These include isolates associated with disease symptoms on *Angophora costata* leaves and stems in New South Wales (NSW); from diseased *Corymbia* spp. in Queensland (QLD); from diseased *Eucalyptus* leaves and shoots in Thailand, Laos and South Africa; and from phloemophagous bark beetles in Tunisia and California and Colorado in the USA. In addition, we obtained a dried culture representing the type of *Q. pusilla*, which had the potential to make DNA based analyses of this species possible.

The primary aim of this study, was to identify all the newly obtained isolates of *Quambalaria* based on DNA sequence comparisons with known species. A second aim was to include a greater number of gene regions than solely the ribosomal internal transcribed spacer (ITS) regions that has been used in past studies, in order to resolve species level questions in *Quambalaria*.

MATERIALS & METHODS

Isolates

Fifty two *Quambalaria*-like isolates were included in this study, as well as one herbarium specimen. An isolate of *Microstroma* was included as an outgroup taxon (**Table 1**). Isolates are maintained in the culture collection (CMW) of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa, the Department of Agriculture Western Australia Plant Pathogen Collection (WAC), Perth, Australia; the collection of M. Kolařik at the Institute of Microbiology (MK and U), ASCR, Prague; the Centraalbureau voor Schimmelcultures (CBS), Utrecht, The Netherlands; the collection of G. Pegg (Q) at the Queensland Department of Primary Industries and Fisheries, Brisbane; and the NSW Plant Pathology Herbarium (DAR), Orange, Australia. Herbarium specimens of the new species were deposited in the National Fungal Collection (PREM), Pretoria, South Africa.

DNA extraction, PCR and DNA sequencing

DNA was extracted from all isolates following the technique of Duong *et al.* (2012). The ITS region was amplified and sequenced using primers ITS1 and ITS4 (White *et al.* 1990).

New primers to amplify the elongation factor 1α (EF) gene region were designed based on the following sequences from GenBank: *Ustilago maydis* XM_751978* (*Ustilaginales*), *Malassezia globosa* XM_001732260* (*Malasseziales*), *Schizophyllum commune* XM_003037215* (*Agaricales*), *Cryptococcus gattii* XM_003197219* (*Tremellales*), *Puccinia graminis f. sp. tritici* XM_003333024 (*Pucciniales*)*, *Puccinia graminis* X73529 (*Pucciniales*), *Pseudozyma flocculosa* GQ922837 (*Ustilaginales*), *Tilletia goloskokovii* DQ832251 (*Tilletiales*), *Cintractia sorghi-vulgaris* DQ028590 (*Ustilaginales*), *Microstroma juglandis* DQ789991 (*Microstromatales*). Sequences originating from whole genomes are indicated by *. The resulting primers, QuamEF-F (5' - AGTGYGGTGGWATYGACAAGC - 3') and QuamEF-R (5' - GTGGTGCATYTCRACNGACTT - 3'), should be applicable to all the above mentioned basidiomycete orders.

PCR, sequencing and DNA purification protocols were exactly as described by Duong *et al.* (2012), with exception that with the EF primers, PCR was performed at an annealing temperature of 55 C, while the annealing temperature for the sequencing PCR was 60 C. Furthermore, when degenerate primers were used, the primer concentrations were 0.4 mM of each primer, while for normal, non degenerate primers, concentrations of 0.2 mM were used. ContigExpress, a component of Vector NTI Advance 11 (Invitrogen, Carlsbad, California), was used to construct consensus sequences.

Phylogenetic analyses

The ITS and EF data were analysed separately from each other. The ITS data set consisted of sequences produced in the present study (**Table 1**) together with reference sequences obtained from NCBI GenBank. Only one EF sequence used as outgroup was available from GenBank. All the other EF sequences were produced as part of the present study.

Both data sets were compiled using MEGA 5.0.5 (Tamura *et al.* 2011) and aligned online using the E-INS-I strategy in MAFFT 6 (Katoh & Toh 2008). Three methods of phylogenetic reconstruction were applied to both data sets. Maximum likelihood (ML) was assessed using PhyML 3.0 online (Guindon *et al.* 2010), Maximum parsimony (MP) in MEGA 5.0.5 (Tamura *et al.* 2011), and for Bayesian analyses (BI) MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) was used. The most appropriate substitution models were selected using the Akaike information criterion (AIC) in MrModelTest 2 (Nylander 2004) for BI, and ModelTest 3.7 (Posada & Crandall 1998) for ML. Branch support for trees obtained by MP and ML was determined using one thousand bootstrap replicates. During BI analyes, four independant runs of 5 million generations each were conducted using duplicate Monte Carlo Markov chain searches with four chains. Trees were saved every 100 generations and burn-in was determined using Tracer 1.4 (http://evolve.zoo.ox.ac.uk/software.html).

RESULTS

Phylogenetic analyses

The numbers of taxa and characters included in the two data sets, the substitution models that were applied in BI and ML, and the statistical values resulting from the different analyses, are presented in **Table 2**. Branch support values are presented in the phylogenetic trees (**Figs 2 & 3**).

Analyses of both the ITS (**Fig. 2**) and EF (**Fig. 3**) data sets resulted in phylogenetic trees showing six distinct clades representing six species. The first clade included the ex-type of *Q. cyanescens* and several isolates previously identified as this species. Isolates obtained in the present study that grouped with *Q. cyanescens* included those from the USA and

Tunisia, as well as two isolates from Laos. A sequence from the study of Cheewangkoon *et al.* (2009) incorrectly labelled as *Penidiella corymbia* was also included

The ITS sequence obtained from the herbarium specimen representing the type of *Q. pusilla*, was identical to two sequences of *Q. simpsonii*, one of which represented the holotype (**Fig. 2**). The same clade was present in both the ITS and EF trees (**Figs 2 & 3**), although with no statistical support in the latter case. Five isolates from Laos and one isolate from Turkey that grouped with *Q. cyanescens* based on ITS, were included.

The third well-supported clade in the ITS tree (**Fig. 1**) included six isolates from *Angophora costata* in New South Wales as well as a sequence from GenBank that came from *Leptospermium juniper* in Victoria, Australia. The six *Angophora* isolates formed an equally well-supported clade in the EF trees (**Fig. 3**), distinct from those representing the known species of *Quambalaria*.

The ex-type isolate of *Q. eucalypti* formed well-supported clades in both trees (**Figs. 2 & 3**) with several other isolates, all from *Eucalyptus.* Several previously unidentified isolates from South Africa, as well as some from Thailand and Laos, were also included in this group.

All previously identified isolates of *Q. coyrecup* grouped together in a distinctly supported clade (*Figs 2 & 3*). A single isolate obtained from *A. costata* in New South Wales was also included in this clade.

All *Q. pitereka* isolates reported previously from Australia and China grouped together with no statistical support in the ITS tree (**Fig. 2**), but with good support in EF tree (**Fig. 3**). Two isolates from Queensland, respectively from *C. ptychocarpa* and *C. tesselaris*, as well as an isolate from *A. costata* in New South Wales, also formed part of this group.

TAXONOMY

DNA sequence analyses revealed a new, well-supported lineage in *Quambalaria* and the isolates residing in this group are described here as a new species. Furthermore, sequences of the herbarium specimen representing the ex-type of *Q. pusilla* were identical to those of *Q. simpsonii*. *Quambalaria pusilla* as the older name has priority and *Q. simpsonii* is thus reduced to synonymy with the former species. .

Quambalaria purpurascens Z.W. de Beer, Marinc. & G.S. Pegg **nom. prov. Fig. 4.**

Conidiophores micronematous or semi-macronematous. *Conidiogenous cells* hyaline, smooth, discrete or integrated, intercalary or terminal, at times reduced to short denticles directly on vegetative hyphae, mostly cylindrical, 9.2 – 41.3 × 1.5 – 2.2 µm, straight, unbranched, erect, with parts consisting of denticles, mostly at apex and swollen or throughout the upper half of the cell without swelling. Denticles sympodial, 1-2 µm long. *Conidia* hyaline, ellipsoidal, pointed towards the base, (2.3)3.9–4.4(6.3) × (1.4–)2.2–2.5(–3.5) µm (average 4.16 × 2.37 µm), aseptate, smooth, guttulated. *Colonies* on MEA circular, flat, powdery, edge entire, mycelia superficial, medium dense, purple pigmentation on media.

Etymology. The name refers to the deep purple pigmentation produced by this species when grown on artificial media.

Specimens examined. AUSTRALIA, New South Wales, Sydney, Waverton Park, from leaf spot on *Angophora costata, collected and isolated by GS Pegg* (PREM PENDING Holotype), culture ex-holotype CBS PENDING = CMW 35351); CMW 35354; CMW 35356; Turramura, Kissing Point Road, from leaf spot on *A. costata, collected and isolated by GS Pegg* (PREM PENDING

Paratype), culture ex-paratype CBS PENDING = CMW 35352); Wollstencraft, Berry Island, from leaf spot on *A. costata, collected and isolated by GS Pegg*, CBS PENDING = CMW 35358; CBS PENDING = CMW 35360.

Quambalaria pusilla (U. Braun & Crous) J.A. Simpson, Australas. Mycol. 19: 61. 2000.
≡ *Sporothrix pusilla* U. Braun & Crous, in Braun, Monogr. *Cercosporella*, *Ramularia* Allied Genera 2: 418. 1998.
= *Quambalaria simpsonii* Cheew. & Crous, Persoonia 23: 77. 2009.

DISCUSSION

DNA sequences for two gene regions were determined for *Quambalaria* isolates from various hosts and geographic locations. Phylogenetic analyses confirmed that the five known species of *Quambalaria* formed monophyletic lineages when compared with published sequences. Our results also revealed the existence of a new species, described here as *Q. purpurascens*. For each of the five previously described species, new host associations and/or first reports from countries on four continents are reported. The sequence data generated in this study also showed that *Q. simpsonii* is the same fungus as *Q. pusilla* and the former species is reduced to synonymy with it

Quambalaria pitereka

Of the six species in the genus, *Q. pitereka* is the most important tree pathogen where it causes severe leaf and shoot blight on commercially planted *Corymbia* spp. in eastern Australia and China (Zhou *et al.* 2008; Pegg *et al.* 2009). In both countries, *Corymbia* spp. are widely planted for sawlog and pulp production (Self *et al.* 2002; Dickinson *et al.* 2004; Zhou *et al.* 2008). The importance of this pathogen is illustrated by the the relatively large number of recent tree improvement studies where a variety of *Corymbia* spp. and hybrids have been screened for resistance to it (Self *et al.* 2002; Lee 2007; Smith *et al.* 2007; Johnson *et al.* 2009; Lee *et al.* 2009; Brawner *et al.* 2011; Pegg *et al.* 2011). Symptoms of *Q. pitereka* include distorted leaves and necrotic lesions, as well as sunken lesions on stems and side branches of young trees (Pegg *et al.* 2008). Repeated infections lead to the loss of leader shoots resulting in stunted, bushy trees (Carnegie 2007a, b; Pegg *et al.* 2008).

The disease caused by *Q. pitereka* was first described in 1955 on *C. maculata* in NSW (Walker & Bertus 1971). In 1960 it was also found on *C. eximia* and in 1971 the causal agent was described as a new species, *Ramularia pitereka* (Walker & Bertus 1971). The rapid expansion of commercial *Corymbia* plantations in NSW and QLD during the 1990's, led to an increased host range and higher disease levels (Carnegie 2007b; Lee 2007). It has also been reported from Western Australia (WA), but it is uncommon and relatively unimportant there (Simpson 2000; Paap *et al.* 2008). The disease was first observed on *C. citriodora* in China in 2007 (Zhou *et al.* 2007). The disease is restricted to a large variety of *Corymbia* spp. and hybrids of these species (**Table 1**). In the present study, we report *Q. pitereka* for the first time from leaf spots and shoot blight on *C. ptychocarpa* and *C. tesselaris* in QLD. Furthermore, we provide the first DNA sequence-based identification of the fungus from a leaf spot on *Angophora costata*, confirming an earlier report by Braun (1998). Inoculation studies by Walker and Bertus (1971), and Pegg *et al.* (2011) showed that *A. costata* is highly susceptible to *Q. pitereka*, while two other *Angophora* spp. were far less susceptible. *Quambalaria pitereka* has never been isolated from *Eucalyptus* in nature. Several attempts to induce disease through artificial inoculation with *Q. pitereka* on *Eucalyptus* spp., have also not resulted in symptoms (Walker & Bertus 1971; Self *et al.* 2002; Pegg *et al.* 2011). This confirms the notion that the fungus is specific to species of *Corymbia*.

DNA sequence data of the ITS region suggest that *Q. pitereka* is genetically highly variable (**Fig. 2**, present study; Pegg *et al.* 2008). EF sequences produced in this study also exihibit some variability among the *Q. pitereka* isolates (**Fig. 3**), but sequences need to be determined for a greater number of isolates to assess the usefullness of this gene in exploring intraspecies variation. The genetic variability also explains the variability in pathogenicity between different isolates (Pegg *et al.* 2011), a fact that needs to be considered in breeding programmes.

Quambalaria eucalypti

Quambalaria eucalypti, infects only *Eucalyptus* spp. and it can be considered the equivalent on *Eucalyptus* of *Q. pitereka* on *Corymbia*. It causes leaf and shoot disease symptoms similar to those caused by *Q. pitereka* on *Corymbia* (Wingfield *et al.* 1993; Pegg *et al.* 2008). The disease was first observed on *E. grandis* growing in clonal hedges in commercial forestry nurseries in the KwaZulu-Natal province of South Africa (Wingfield *et al.* 1993). It was later found to cause substantial leaf and shoot damage, as well as stem cankers, on one year-old *E. nitens* trees in Mpumalanga province of South Africa (Roux *et al.* 2006). In South America, the disease was first observed on *Eucalyptus* in Uruguay (Bettucci *et al.* 1999), and shortly afterwards in Brazil (Alfenas *et al.* 2001). The first report of a possible host jump of *Q. eucalypti* came from Uruguay, where it was isolated from leaf lesions on a native myrtaceous host tree, *Myrceugenia glaucescens* (Pérez *et al.* 2008). It has since spread to become one of the most serious diseases in *Eucalyptus* nurseries in Brazil (Andrade *et al.* 2005, 2007; Ferreira *et al.* 2008; Mafia *et al.* 2009).

Although Australia seems to be the most obvious area of origin for *Q. eucalypti*, it was only found for the first time in that country in NSW in 2004 (Carnegie 2007a). Pegg *et al.* (2008) later also reported it from QLD. The discovery of *Q. eucalypti* in the present study from *Eucalyptus* leaves in both Thailand and Laos, represents the first report of this fungus from Southeast Asia. This might have significant implications to the forestry industry on that continent. Especially for neighboring China, where more than 1 million hectares of *Eucalyptus* trees, mostly hybrids of *E. urophylla* with species such as *E. grandis,* have been planted during the past decade (Zhou *et al.* 2008).

Quambalaria pusilla

Quambalaria pusilla has been isolated only from spots on a single collection of exotic *E. camaldulensis* leaves in Thailand (Braun 1998). Since the ex-type culture of *Q. pusilla* was lost due to contamination (De Beer *et al.* 2006), DNA sequences could not be obtained for it. However, Dr Uwe Braun made a dried culture of the ex-type isolate avaiable to us for DNA analyses. The sequences obtained from this specimen were identical to those of two isolates of *Q. simpsonii*, a species described from *Eucalyptus* leaves in Thailand, similar to *Q. pusilla*, but also from *E. tintinnans* from Australia's Northern Territory (NT) (Cheewangkoon *et al.* 2009). The synonymy between the two species implies that *Q. pusilla* is also present in Australia. Furthermore, we report this fungus from *Eucalyptus* leaves in Laos, which means that it has a wider distribution in Southeast Asia than previously recognized. However, apart from the fact that this species was isolated from leave spots on *Eucalyptus*, nothing is known about its pathogenicity, or thus the potential risks it might pose to the forestry industry.

Quambalaria coyrecup

The first report of a *Quambalaria* species dates back to 1935, when H.A. Pittman submitted some cultures from what he described as a stem canker disease on *C. ficifolia* and *C. calophylla* in WA, to Kew Botanical Gardens for identification (Walker & Bertus 1971). In his reply to Pittman, the director of Kew Botanical Gardens, S.F. Ashby, included a preliminary description and name for the fungus (*Sporotrichum destructor*) provided by E.W. Mason (Ashby 1936). Inoculations of healthy trees with the fungus confirmed that it was highly pathogenic to both tree species on which it was first found. However, the species name was invalid as it was never formally published. The disease was eventually described in more detail by Cass Smith (1970).

Paap *et al.* (2008) found the same fungus from stem cankers of adult *C. calophylla* trees and provided it with a valid species name, *Q. coyrecup*. Pegg *et al.* (2008) reported the same species from stem cankers on *C. polycarpa* in the NT. In the present study, we report this fungus for the first time from a stem canker on *A. costata* in NSW, but it remains known only from Australia.

Quambalaria purpurascens

Amin *et al.* (2010) reported an endophytic fungus from asymptomatic *Leptospermum junipae* in Victoria as an unnamed species of *Quambalaria*. The ITS sequence of their isolate matches those of several isolates obtained during the present study from leaf spots on *A. costata* in NSW (**Fig. 2**). Together, these isolates formed a well-supported lineage, also present in the EF tree (**Fig. 3**), distinct from other *Quambalaria* species. As is the case for *Q. coyrecup*, this species is thus known only from Australia, and nothing more is known about its pathogenicity or host range.

Quambalaria cyanescens

Quambalaria cyanescens was first described by from human skin and air in Europe (De Hoog & De Vries 1973). Surprisingly, an isolate of the same species from *E. pauciflora* in NSW was sent to CBS for identification in 1973 (De Beer *et al.* 2006). Pegg *et al.* (2008) reported the fungus from discrete lesions on woody stems of native *Corymbia* in QLD and NSW, while Paap *et al.* (2008) reported it from shoots, leaves, stem cankers and asymptomatic material of *Corymbia* in WA. In this study, the fungus was isolated from leaf spots on *A. costata* in NSW, representing the first report of this species from *Angophora*. It was also present on leaf lesions on *Eucalyptus* in Laos, which represents the first report of this species on a eucalypt outside of Australia.

Quambalaria cyanescens is unique among the species of this genus in that it does not have a host range restricted to the *Myrtaceae*. For example, analyses in this study showed that an unpublished ITS sequence from *Ipomoea carnea* in India also represents this species (**Fig. 2**), as well as an isolate from red kojic rice in China (Zhang *et al.* 2011). The enigmatic occurrence of *Q. cyanescens* with bark beetles has been revealed in an exstensive study by Kolařík *et al.* (2006), who isolated the fungus from several countries in the Mediterranean, Hungary and Bulgaria. In the present study we found the species from more hardwood infesting bark beetles in Tunisia, California and Colorado. To the best of our knowledge, these reports represent the first confirmation of the occurrence of *Q. cyanescens* from hosts in the USA other than from human tissue (**Table 1**). Kolařík *et al.* (2006) mentioned a number of physiological characters that might enable *Q. cyanescens* to live in close association with beetle and other fungal species in bark beetle galleries. However, the exact role of this species in these relationships remains unclear.

Similar to its bark beetle associations, the wide geographic distribution and clinical manifestation of *Q. cyanescens* in Europe and the USA is somewhat enigmatic (Summerbell *et al.* 1993; Sigler *et al.* 1990; Middelhoven *et al.* 2000). It appears to be an opportunistic pathogen infecting mostly immunocompromised humans (Jackson *et al.* 1990; Sigler *et al.* 1990; Tambini *et al.* 1996; Grossi *et al.* 2000), possibly originating in the soil (Lièvremont *et al.* 1996), air (De Hoog & De Vries 1973) or even food such as processed oats (Da Silva *et al.* (1999), red kojic rice (Zhang *et al.* 2011) or fruit juice (Middelhoven *et al.* 2000).

Concluding remarks

Australia is the only continent from which all six known *Quambalaria* spp. have been reported. Together with this fact, the seemingly high genetic diversity of for example *Q. pitereka* suggests that this country is the centre of origin of these species, and also the centre of diversity for the genus. Sexual reproduction has not been observed for any species of *Quambalaria*, but its basidiospores might masquerade as conidia. This would be similar to the situation in the closely related genera such as *Sympodiomycopsis*. Furthermore, all the species are associated strictly with myrtaceous hosts in Australia, from where they were apparently introduced into eucalypt growing areas in Southern Africa, South America and Southeast Asia.

Five of the species of *Quambalaria* are restricted to the *Myrtaceae*, with *Q. eucalypti*, *Q. pitereka*, *Q. pusilla*, and *Q. purpurascens* causing leaf and shoot damage, and *Q. coyrecup* causing stem cankers. The sixth species, *Q. cyanescens*, has been reported from both cankers and leaves and shoots in Australia, often occurring together with other *Quambalaria* spp. on the same infected tissue (Paap *et al.* 2008), which was also the case on material from Laos included in the present study. *Quambalaria cyanescens* is the only species that has been reported from all continents (apart from Antarctica), but outside Australia it has been isolated from soil, air, hardwood-infesting bark beetles and diseased humans. It is clear that there are many aspects of the biology and ecology of *Quambalaria* that are poorly understood and worthy of further research efforts.

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Table 1 Geographic distribution and hosts of *Quambalaria* spp.

Species	Country	Host	Reference
Q. coyrecup	[1]Australia, NSW	*Angophora costata*	present study
	Australia, NT	*Corymbia polycarpa*	Pegg et al. 2008
	Australia, WA	*C. calophylla*	Ashby 1936; Cass Smith 1970; Paap et al. 2008
	Australia, WA	*C. ficifolia*	Ashby 1936; Cass Smith 1970; Paap et al. 2008
Q. cyanescens	Australia, NSW	*A. costata*	present study
	Australia, NSW	*Eucalyptus pauciflora*	De Beer et al. 2006; Pegg et al. 2008
	Australia, QLD	*C. citriodora*	Pegg et al. 2008; present study
	Australia, QLD	*C. variegata*	Pegg et al. 2008
	Australia, WA	*C. calophylla*	Paap et al. 2008; Pegg et al. 2008
	Australia, WA	*C. ficifolia*	Paap et al. 2008
	Brazil	processed oat	Da Silva *et al.* 1999
	Bulgaria	*Quercus* sp.*	Kolařík et al. 2006
	Bulgaria	*Tilia cordata**	Kolařík et al. 2006
	Canary Islands	*Cuscuta approximata* (dodder)	Middelhoven 1997
	China, Shandong	red kojic rice	Zhang et al. 2011
	Croatia	*Euphorbia charracis**	Kolařík et al. 2006
	Croatia	*Olea europea**	Kolařík et al. 2006
	Finland	human skin	De Hoog & De Vries 1973
	Hungary	*Carpinus betulus**	Kolařík et al. 2006
	Israel	pomegranate product	Middelhoven *et al.* 2000
	India	*Ipomoea carnea*	present study
	Italy	human lung	Tambini *et al.* 1995; Middelhoven *et al.* 2000
	Laos	*Eucalyptus* sp.	present study
	Morocco	air	Sigler *et al.* 1990
	Netherlands	human skin, air	De Hoog & De Vries 1973; De Beer et al. 2006
	Spain	*O. europea**	Kolařík et al. 2006
	Spain	soil	Liévremont *et al.* 1996
	Syria	*Amygdalis communis**	Kolařík et al. 2006
	Syria	*O. europea**	Kolařík et al. 2006
	Tunisia	*Arbutus andrachne**	present study
	Turkey	*F. carica**	Kolařík et al. 2006
	Turkey	*Malus domestica**	Kolařík et al. 2006
	Turkey	*Pistacia vera**	Kolařík et al. 2006
	USA, California	*Pinus angustifolia**	present study
	USA, California	*Prunus* sp.*	present study
	USA, California	*Pseudotsuga douglasii**	present study
	USA, California	*Q. acrifolia**	present study
	USA, California	*Q. kelloggii**	present study
	USA, Colorado	*Fraxinus* sp.*	present study
	USA, Connecticut	human blood	Sigler *et al.* 1990
	USA, Louisiana	human lungs	Jackson *et al.* 1990
	USA, Maine	human blood	Sigler *et al.* 1990
	USA, Michigan	human blood	Sigler *et al.* 1990
	USA, New York	human blood, finger	Sigler *et al.* 1990
	USA, Texas	human blood	Sigler *et al.* 1990
	USA, Virginia	human blood	Sigler *et al.* 1990
Q. eucalypti	Australia, NSW	*E. dunnii*	Carnegie 2007a; Pegg et al. 2008
	Australia, NSW	*E. grandis*	Carnegie 2007a, b; Pegg et al. 2008
	Australia, NSW	*E. longirostrata*	Carnegie 2007a; Pegg et al. 2008
	Australia, QLD	*C. torelliana x C. citriodora* s. *variegata*	Pegg et al. 2008
	Australia, QLD	*E. grandis*	Pegg et al. 2008
	Australia, QLD	*E. longirostrata*	Pegg et al. 2008
	Brazil	*E. globulus*	Alfenas *et al.* 2001; Mafia *et al.* 2009
	Brazil	*E. saligna x E. maidenii*	Alfenas *et al.* 2001
	Brazil	*E. urophylla x E. maidenii*	Mafia *et al.* 2009
	Laos	*Eucalyptus* sp.	present study

[1] Australian states: NSW = New South Wales, NT = Northern Territory, QLD = Queensland; VC = Victoria; WA = Western Australia

Table 1 (Continued) Geographic distribution and hosts of *Quambalaria* spp.

Species	**Country**	**Host**	**Reference**
Q. eucalypti	South Africa	*E. grandis*	Wingfield *et al.* 1993; De Beer et al. 2006; Roux et al. 2006
	South Africa	*E. grandis x E. camaldulensis*	De Beer et al. 2006; Roux et al. 2006
	South Africa	*E. nitens*	Roux et al. 2006
	Thailand	*Eucalyptus sp.*	present study
	Uruguay	*E. globulus*	Bettucci *et al.* 1999
	Uruguay	*Myrceugenia glaucescens*	Pérez et al. 2008
Q. pitereka	[1] Australia, NSW	*A. costata*	Braun 1998; present study
	Australia, NSW	*C. citriodora*	Simpson 2000; Pegg et al. 2008
	Australia, NSW	*C. citriodora s. variegata*	Carnegie 2007b; Johnson et al. 2008; Pegg et al. 2008
	Australia, NSW	*C. eximia*	Walker & Bertus 1971; Simpson 2000; Paap et al. 2008
	Australia, NSW	*C. henryi*	Simpson 2000; Pegg et al. 2008
	Australia, NSW	*C. maculata*	Walker & Bertus 1971; Simpson 2000; Pegg et al. 2008
	Australia, QLD	*C. citriodora*	Pegg et al. 2008;
	Australia, QLD	*C. citriodora s. citriodora*	Simpson 2000; Dickinson *et al.* 2004; Pegg et al. 2008
	Australia, QLD	*C. citriodora s. variegata*	Simpson 2000; Dickinson *et al.* 2004; Pegg et al. 2008
	Australia, QLD	*C. henryi*	Dickinson *et al.* 2004; Pegg et al. 2008
	Australia, QLD	*C. ptychocarpa*	present study
	Australia, QLD	*C. tesselaris*	present study
	Australia, QLD	*C. torelliana*	Pegg et al. 2008
	Australia, QLD	*C. torelliana* × *C. citriodora s. citriodora*	Zhou et al. 2007; Pegg et al. 2008
	Australia, QLD	*C. torelliana* × *C. henryi*	Pegg et al. 2008
	Australia, QLD	*C. torelliana x C. citriodora s. variegata*	Pegg et al. 2008
	Australia, WA	*C. calophylla*	Paap et al. 2008
	Australia, WA	*C. ficifolia*	Braun 1998; Simpson 2000; Paap et al. 2008
	China, GuangDong	*C. citriodora*	Zhou et al. 2007; Pegg et al. 2008;
Q. purpurascens nom. prov.	Australia, NSW	*A. costata*	present study
	Australia, VC	*Leptospermum junipae*	Amin *et al.* 2010 (as *Quambalaria* sp.)
Q. pusilla	Laos	*Eucalyptus* sp.	present study
	Thailand	*E. camaldulensis*	Braun 1998; Cheewangkoon et al. 2009
	Australia, NT	*E. tintinnans*	Cheewangkoon *et al.* 2009 (as *Q. simpsonii*)

[1] Australian states: NSW = New South Wales, NT = Northern Territory, QLD = Queensland; VC = Victoria; WA = Western Australia

Table 2 Isolates used in this study. Genbank numbers for sequences obtained in this study are printed in bold type.

Species	[a]CMW	[b]Other	Type	Host	Insect or symptom	Region	Country	Collector	ITS	EF
Q. coyrecup	35361	Q480		*Angophora costata*	stem canker	NSW	Australia	GS Pegg	**PENDING**	**PENDING**
	37029	WAC12947	T	*Corymbia calophylla*	stem canker	WA	Australia	T Paap	DQ823431	**PENDING**
	37030	WAC12949		*C. calophylla*	stem canker	WA	Australia	T Paap	DQ823432	**PENDING**
Q. cyanescens	35349	Q478		*A. costata*	leaf spot	NSW	Australia	GS Pegg	**PENDING**	**PENDING**
	35357	Q796		*Corymbia* sp.	leaf spot	QLD	Australia	GS Pegg	**PENDING**	**PENDING**
	35359	Q472		*A. costata*	leaf spot	NSW	Australia	GS Pegg	**PENDING**	**PENDING**
	37505			*Eucalyptus* sp.	leaf spot		Laos	ZW de Beer	**PENDING**	**PENDING**
	37508			*Eucalyptus* sp.	leaf spot		Laos	ZW de Beer	**PENDING**	**PENDING**
	37529	MK1855		*Arbutus andrachne*	scolytid beetle		Tunisia	M Kolařík	**PENDING**	**PENDING**
	37530	U16		*Quercus kelloggii*	*Pseudopityophthorus pubinpennis*	California	USA	M Kolařík	**PENDING**	**PENDING**
		MK617		*Carpinus betulus*	*Scolytus carpini*		Hungary	M Kolařík	AM261923	**PENDING**
		MK742		*Pistacia vera*	*Chaetoptelius vestitus*	Icel Province	Turkey	M Kolařík	AM261920	**PENDING**
		MK808		*Olea europea*	*Phleotribus scarabeoides*		Syria	M Kolařík	AM261921	**PENDING**
		U100		*Q. acrifolia*	*P. pubinpennis*	California	USA	M Kolařík	**PENDING**	
		U105		*Prunus* sp.	*S. rugulosus*	California	USA	M Kolařík	**PENDING**	
		U110		*Prunus* sp.	*S. rugulosus, Pseudothysanoes hopkinsi*	California	USA	M Kolařík	**PENDING**	
		U121		*Pinus angustifolia*	Cerambycid beetle	California	USA	M Kolařík	**PENDING**	
		U144		*Pseudotsuga douglasii*	*Orthotomicus latidens*	California	USA	M Kolařík	**PENDING**	
		U161		*Fraxinus* sp.	*Hylesinus oregonus*	Colorado	USA	M Kolařík, N Tisserat	**PENDING**	
		U163		*Fraxinus* sp.	*H. oregonus*	Colorado	USA	M Kolařík, N Tisserat	**PENDING**	
		U182		*Fraxinus* sp.	*H. oregonus*	Colorado	USA	M Kolařík, N Tisserat	**PENDING**	
Q. eucalypti	919				leaf spot/ shoot blight	KwaZulu-Natal	South Africa	MJ Wingfield	**PENDING**	**PENDING**
	1101	CBS118844	T	*E. grandis*	leaf spot/ shoot blight	KwaZulu-Natal	South Africa	MJ Wingfield	DQ317625	**PENDING**
	11679			*E. grandis* clone	leaf spot/ shoot blight	KwaZulu-Natal	South Africa	L Lombard	**PENDING**	**PENDING**
	11681			*E. grandis* clone	leaf spot/ shoot blight	KwaZulu-Natal	South Africa	L Lombard	**PENDING**	**PENDING**
	11682			*E. grandis* clone	leaf spot/ shoot blight	KwaZulu-Natal	South Africa	L Lombard	**PENDING**	**PENDING**
	17252	CBS118615		*E. nitens*	leaf spot/ shoot blight	Mpumalanga	South Africa	J Roux	DQ317609	**PENDING**
	37509			*Eucalyptus* sp.	leaf spot/ shoot blight		Laos	ZW de Beer	**PENDING**	
	37522			*Eucalyptus* sp.	leaf spot/ shoot blight		South Africa	J Roux	**PENDING**	**PENDING**
	37523			*Eucalyptus* sp.	leaf spot/ shoot blight		South Africa	J Roux	**PENDING**	**PENDING**
	37524			*Eucalyptus* sp.	leaf spot/ shoot blight		Thailand	ZW de Beer	**PENDING**	
	37525			*Eucalyptus* sp.	leaf spot/ shoot blight		Thailand	ZW de Beer	**PENDING**	
	37526			*Eucalyptus* sp.	leaf spot/ shoot blight		Thailand	ZW de Beer	**PENDING**	
Q. pitereka	5326				leaf spot/ shoot blight	QLD	Australia		**PENDING**	
	23610			*C. citriodora*	leaf spot/ shoot blight	GuangDong	China	YJ Xie	EF427372	**PENDING**

Table 2 Isolates used in this study (continued). Genbank numbers for sequences obtained in this study are printed in bold type.

Species	[a]CMW	[b]Other	Type	Host	Insect	Region	Country	Collector	ITS	EF
Q. pitereka	23611			*C. citriodora*	leaf spot/ shoot blight	GuangDong	China	YJ Xie	EF427373	**PENDING**
	23612			*C. citriodora*	leaf spot/ shoot blight	GuangDong	China	YJ Xie	EF427374	**PENDING**
	35350	Q482		*A. costata*	leaf spot	NSW	Australia	GS Pegg	**PENDING**	
	35353	Q497		*C. tessellaris*	leaf spot/ shoot blight	QLD	Australia	GS Pegg	**PENDING**	**PENDING**
	35355	Q495		*C. ptychocarpa*	leaf spot	QLD	Australia	GS Pegg	**PENDING**	**PENDING**
	35362	DAR19773	T	*C. eximia*	shoot blight	NSW	Australia	AJ Bertus, J Walker	DQ823423	**PENDING**
Q. purpurascens nom. prov..	35351	Q476	T	*A. costata*	leaf spot	NSW	Australia	GS Pegg	**PENDING**	**PENDING**
	35352	Q481		*A. costata*	leaf spot	NSW	Australia	GS Pegg	**PENDING**	**PENDING**
	35354	Q471		*A. costata*	leaf spot	NSW	Australia	GS Pegg	**PENDING**	**PENDING**
	35356	Q473		*A. costata*	leaf spot	NSW	Australia	GS Pegg	**PENDING**	**PENDING**
	35358	Q470		*A. costata*	leaf spot	NSW	Australia	GS Pegg	**PENDING**	**PENDING**
	35360	Q469		*A. costata*	leaf spot	NSW	Australia	GS Pegg	**PENDING**	**PENDING**
Q. pusilla		Herb. number?	T	*E. camaldulensis*	leaf spot		Thailand	MJ Wingfield	**PENDING**	**PENDING**
	37503			*Eucalyptus* sp.	leaf spot		Laos	ZW de Beer	**PENDING**	**PENDING**
	37504			*Eucalyptus* sp.	leaf spot		Laos	ZW de Beer	**PENDING**	
	37506			*Eucalyptus* sp.	leaf spot		Laos	ZW de Beer	**PENDING**	**PENDING**
	37510			*Eucalyptus* sp.	leaf spot		Laos	ZW de Beer	**PENDING**	
	37511			*Eucalyptus* sp.	leaf spot		Laos	ZW de Beer	**PENDING**	**PENDING**
***Microstroma* sp.**	37527			*Albizia mucronata*	leaf spot		South Africa	D Begerow	**PENDING**	**PENDING**

[a]CMW = Culture Collection of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa;

[b]WAC, Department of Agriculture Western Australia Plant Pathogen Collection, Perth, Australia; MK and U =collection of M. Kolařik at the Institute of Microbiology, ASCR, Prague; CBS = Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; Q = collection of G. Pegg at the Queensland Department of Primary Industries and Fisheries, Brisbane; DAR = NSW Plant Pathology Herbarium, Orange, Australia.

T = ex-type isolates.

Table 3 Parameters used during phylogenetic analyses of the different data sets, and statistical values resulting from the analyses.

	Dataset	ITS	EF
No. of taxa		110	40
No. of characters	**Total**	608	538
MP	**PIC**	83	53
	No. of trees	4510	38
	Tree length	272	142
	CI	0.743	0.753
	RI	0.962	0.913
ML & BI	**Subst. model**	HKY+I+G	TrN+G
	Gamma	0.45	0.219
	P-inv	0	0
BI	**Burn-in**	100	100

PIC = number of parsimony informative characters; CI = consistency index; RI = retention index; Subst. model = best fit substitution model; Gamma = gamma distribution shape parameter; P-inv = proportion of invariable sites.

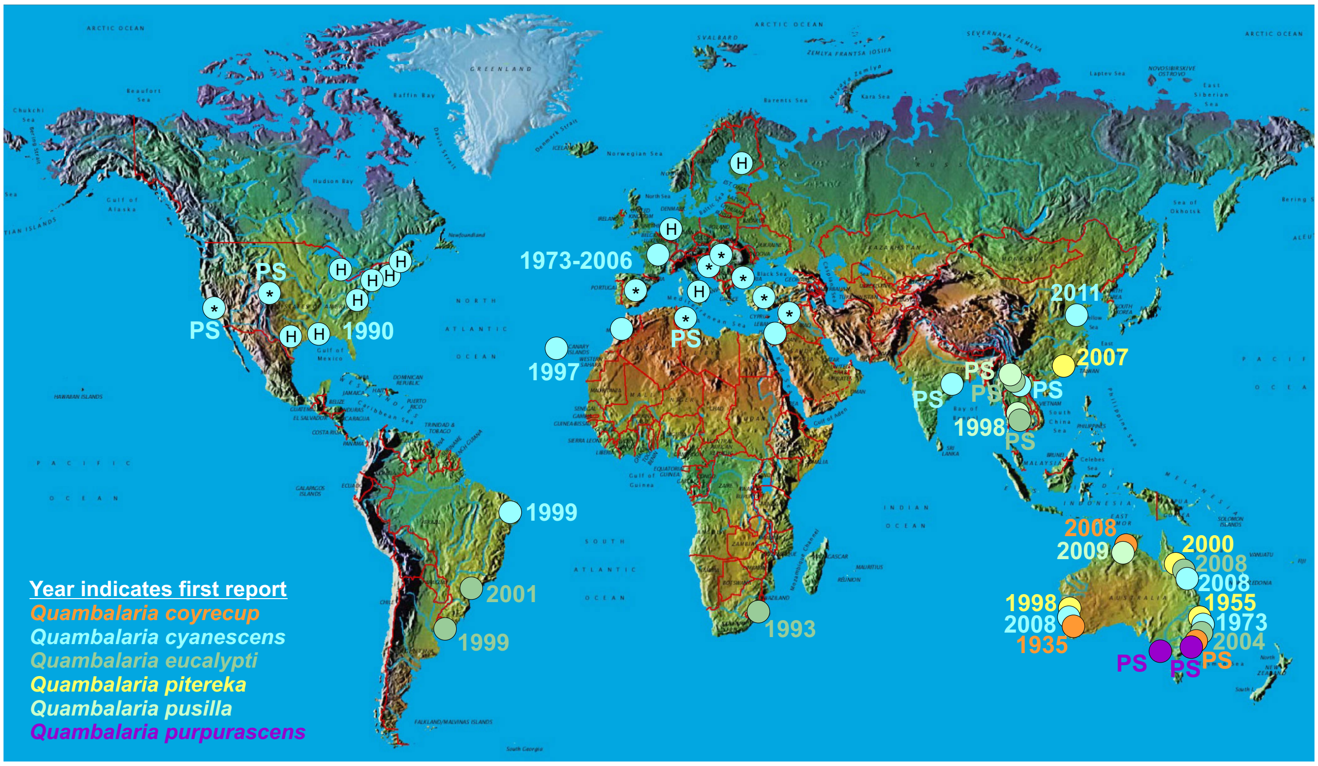


Fig. 1 World map showing the global distribution of *Quambalaria* spp. The year of the first report of each species from a country is presented next to the colour-coded circle representing the species. PS = present study; H = isolated from human tissue; * associated with insect

Fig. 2 Phylogram resulting from ML analyses of the ITS sequences of all species of *Quambalaria*. Bold type indicates isolates for which sequences were generated in the present study. T indicates ex-type isolates.

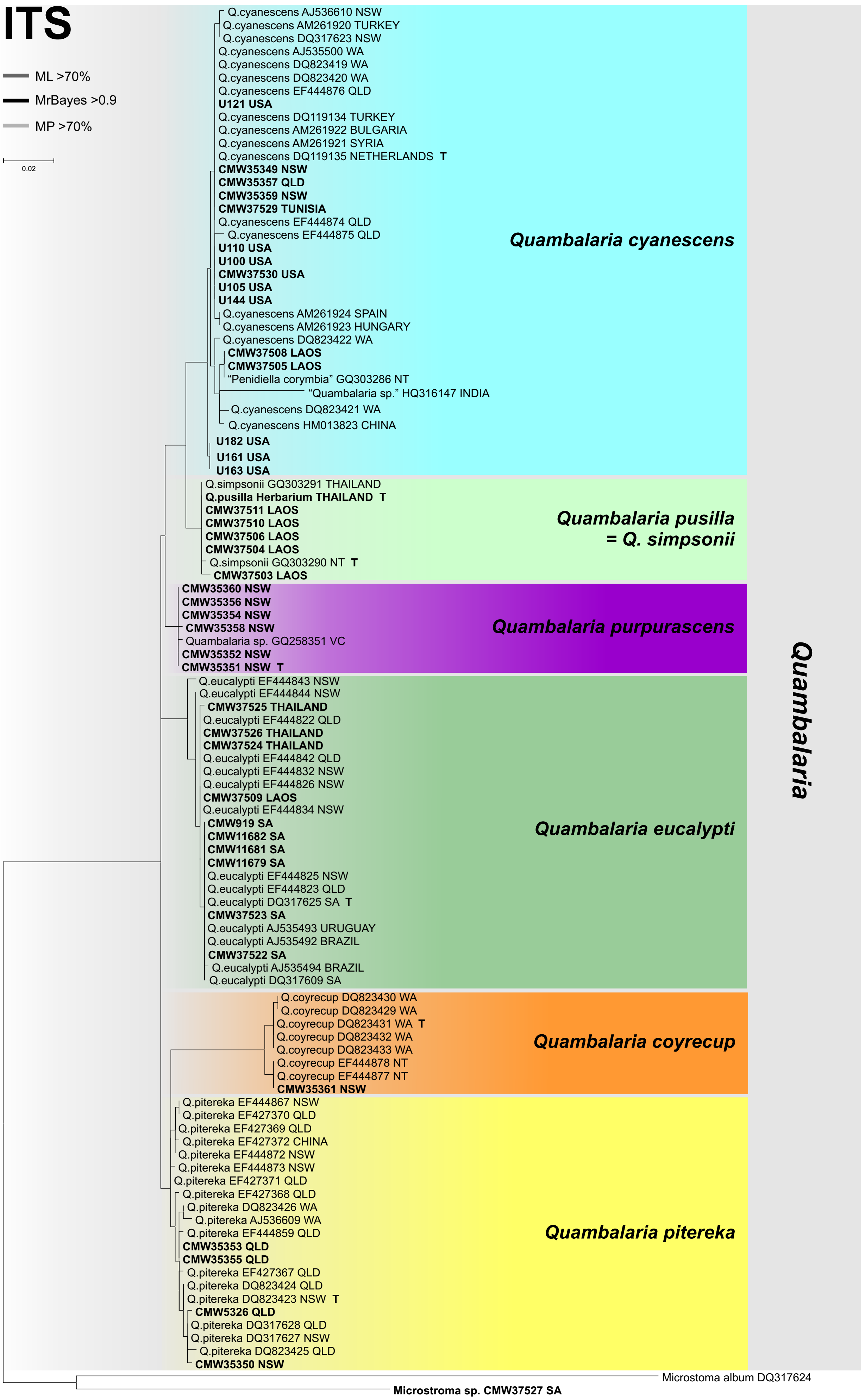
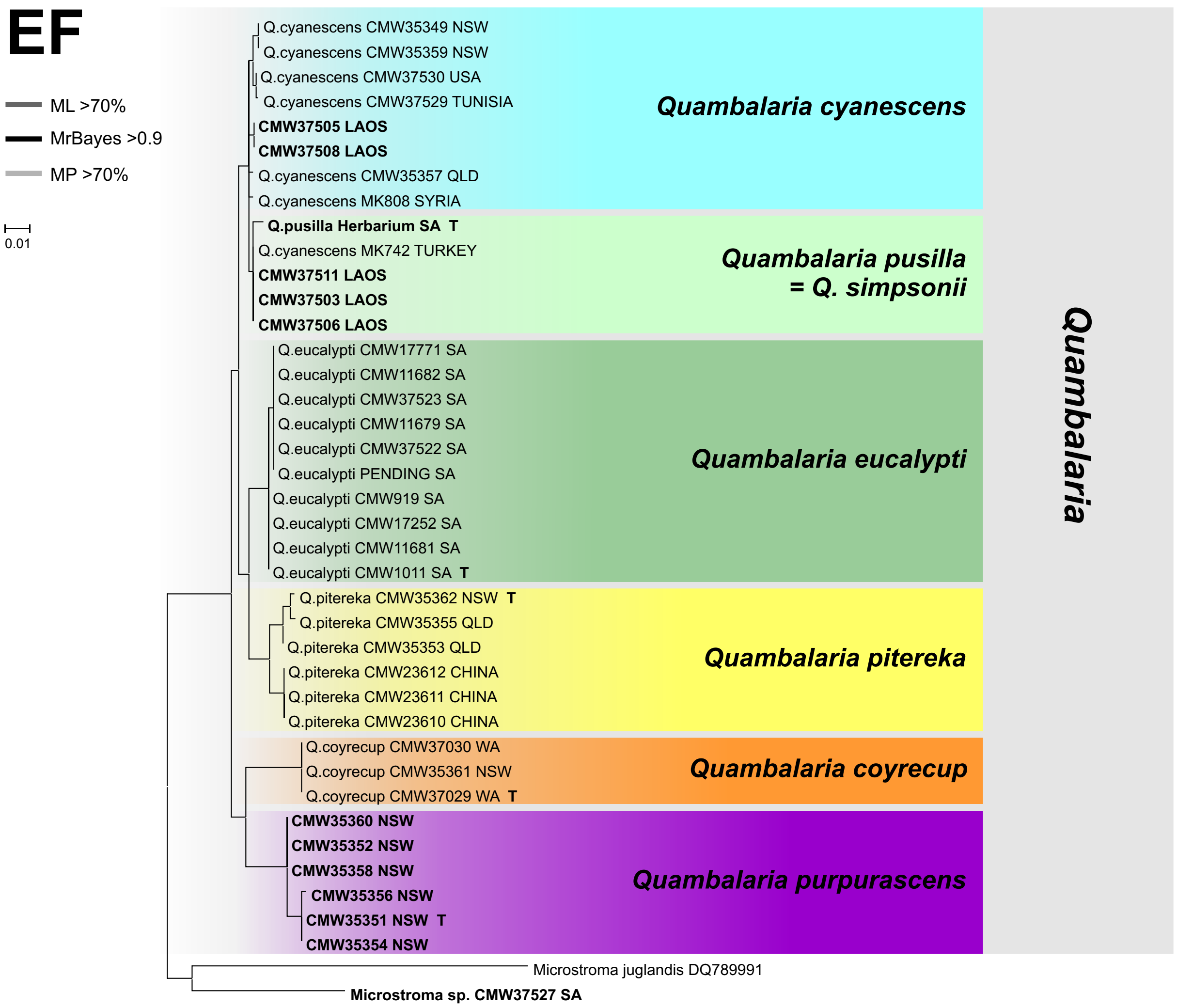

ITS
ML >70%
MrBayes >0.9
MP >70%
0.02
Q.cyanescens AJ536610 NSW
Q.cyanescens AM261920 TURKEY
Q.cyanescens DQ317623 NSW
Q.cyanescens AJ535500 WA
Q.cyanescens DQ823419 WA
Q.cyanescens DQ823420 WA
Q.cyanescens EF444876 QLD
U121 USA
Q.cyanescens DQ119134 TURKEY
Q.cyanescens AM261922 BULGARIA
Q.cyanescens AM261921 SYRIA
Q.cyanescens DQ119135 NETHERLANDS T
CMW35349 NSW
CMW35357 QLD
CMW35359 NSW
CMW37529 TUNISIA
Q.cyanescens EF444874 QLD
Q.cyanescens EF444875 QLD
U110 USA
U100 USA
CMW37530 USA
U105 USA
U144 USA
Q.cyanescens AM261924 SPAIN
Q.cyanescens AM261923 HUNGARY
Q.cyanescens DQ823422 WA
CMW37508 LAOS
CMW37505 LAOS
"Penidiella corymbia" GQ303286 NT
"Quambalaria sp." HQ316147 INDIA
Q.cyanescens DQ823421 WA
Q.cyanescens HM013823 CHINA
U182 USA
U161 USA
U163 USA
Quambalaria cyanescens
Q.simpsonii GQ303291 THAILAND
Q.pusilla Herbarium THAILAND T
CMW37511 LAOS
CMW37510 LAOS
CMW37506 LAOS
CMW37504 LAOS
Q.simpsonii GQ303290 NT T
CMW37503 LAOS
Quambalaria pusilla
= Q. simpsonii
CMW35360 NSW
CMW35356 NSW
CMW35354 NSW
CMW35358 NSW
Quambalaria sp. GQ258351 VC
CMW35352 NSW
CMW35351 NSW T
Quambalaria purpurascens
Q.eucalypti EF444843 NSW
Q.eucalypti EF444844 NSW
CMW37525 THAILAND
Q.eucalypti EF444822 QLD
CMW37526 THAILAND
CMW37524 THAILAND
Q.eucalypti EF444842 QLD
Q.eucalypti EF444832 NSW
Q.eucalypti EF444826 NSW
CMW37509 LAOS
Q.eucalypti EF444834 NSW
CMW919 SA
CMW11682 SA
CMW11681 SA
CMW11679 SA
Q.eucalypti EF444825 NSW
Q.eucalypti EF444823 QLD
Q.eucalypti DQ317625 SA T
CMW37523 SA
Q.eucalypti AJ535493 URUGUAY
Q.eucalypti AJ535492 BRAZIL
CMW37522 SA
Q.eucalypti AJ535494 BRAZIL
Q.eucalypti DQ317609 SA
Quambalaria eucalypti
Q.coyrecup DQ823430 WA
Q.coyrecup DQ823429 WA
Q.coyrecup DQ823431 WA T
Q.coyrecup DQ823432 WA
Q.coyrecup DQ823433 WA
Q.coyrecup EF444878 NT
Q.coyrecup EF444877 NT
CMW35361 NSW
Quambalaria coyrecup
Q.pitereka EF444867 NSW
Q.pitereka EF427370 QLD
Q.pitereka EF427369 QLD
Q.pitereka EF427372 CHINA
Q.pitereka EF444872 NSW
Q.pitereka EF444873 NSW
Q.pitereka EF427371 QLD
Q.pitereka EF427368 QLD
Q.pitereka DQ823426 WA
Q.pitereka AJ536609 WA
Q.pitereka EF444859 QLD
CMW35353 QLD
CMW35355 QLD
Q.pitereka EF427367 QLD
Q.pitereka DQ823424 QLD
Q.pitereka DQ823423 NSW T
CMW5326 QLD
Q.pitereka DQ317628 QLD
Q.pitereka DQ317627 NSW
Q.pitereka DQ823425 QLD
CMW35350 NSW
Quambalaria pitereka
Quambalaria
Microstoma album DQ317624
Microstroma sp. CMW37527 SA

Fig. 3 Phylogram resulting from ML analyses of the EF sequences of all species of *Quambalaria*. Bold type indicates isolates for which sequences were generated in the present study. T indicates ex-type isolates.


EF
ML >70%
MrBayes >0.9
MP >70%
0.01
Q.cyanescens CMW35349 NSW
Q.cyanescens CMW35359 NSW
Q.cyanescens CMW37530 USA
Q.cyanescens CMW37529 TUNISIA
CMW37505 LAOS
CMW37508 LAOS
Q.cyanescens CMW35357 QLD
Q.cyanescens MK808 SYRIA
Quambalaria cyanescens
Q.pusilla Herbarium SA T
Q.cyanescens MK742 TURKEY
CMW37511 LAOS
CMW37503 LAOS
CMW37506 LAOS
Quambalaria pusilla
= Q. simpsonii
Q.eucalypti CMW17771 SA
Q.eucalypti CMW11682 SA
Q.eucalypti CMW37523 SA
Q.eucalypti CMW11679 SA
Q.eucalypti CMW37522 SA
Q.eucalypti PENDING SA
Q.eucalypti CMW919 SA
Q.eucalypti CMW17252 SA
Q.eucalypti CMW11681 SA
Q.eucalypti CMW1011 SA T
Quambalaria eucalypti
Q.pitereka CMW35362 NSW T
Q.pitereka CMW35355 QLD
Q.pitereka CMW35353 QLD
Q.pitereka CMW23612 CHINA
Q.pitereka CMW23611 CHINA
Q.pitereka CMW23610 CHINA
Quambalaria pitereka
Q.coyrecup CMW37030 WA
Q.coyrecup CMW35361 NSW
Q.coyrecup CMW37029 WA T
Quambalaria coyrecup
CMW35360 NSW
CMW35352 NSW
CMW35358 NSW
CMW35356 NSW
CMW35351 NSW T
CMW35354 NSW
Quambalaria purpurascens
Quambalaria
Microstroma juglandis DQ789991
Microstroma sp. CMW37527 SA

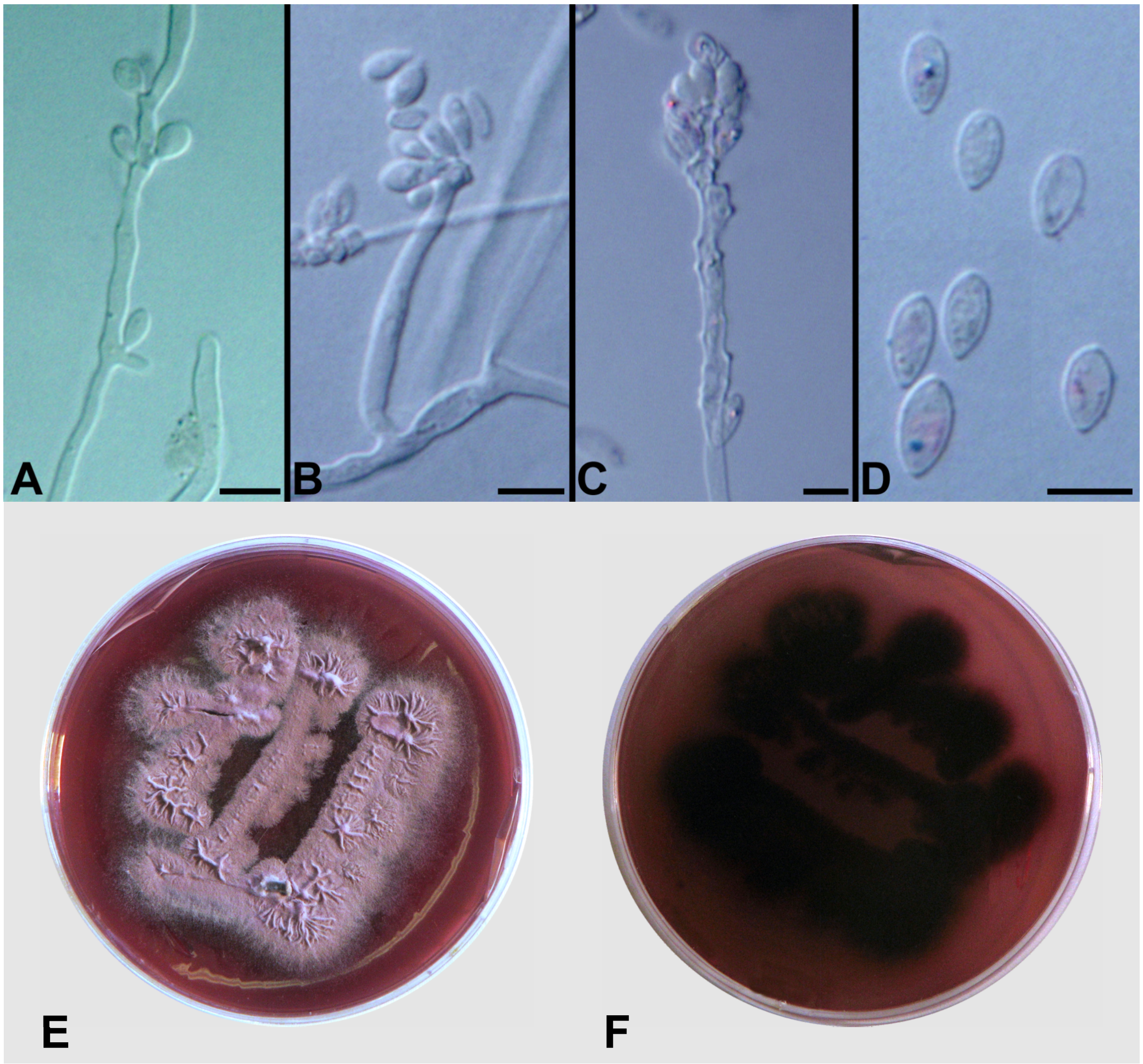


Fig. 4 Morphological characters of *Q. purpurascens* nom. prov. **A.** Denticles borne directly on vegetative hypha. **B.** Conidiogenous cell with a swollen apex bearing several denticles. **C.** Denticles borne throughout the conidiogenous cell. **D.** Conidia. **E.** Colony on MEA after 10 days from above, and **F.** below, showing the diffusion of purple pigment in the medium. Scale bars AD = 5 µm

Summary

Summary

The ophiostomatoid fungi included more than 450 species of ascomycetes specifically adapted for insect dispersal. Many of these species have a significant economic impact as sapstaining fungi or tree pathogens harmful to forestry industries, but some are also as opportunistic human pathogens. DNA based studies in recent years have shown that the majority of these fungi belonged in either the *Ophiostomatales* or *Microascales* (*Sordariomycetes*)*,* with a few *Sporothrix* spp. grouping in the *Microstromatales* (*Ustilaginomycetes*). However, most phylogenetic studies have focussed on restricted numbers of taxa sharing similar morphology. The aim of the studies in this thesis was to reconsider the taxonomy of all the ophiostomatoid fungi at the order and family levels, and the status of genera and species with sporothrix-like anamorphs in the *Ophiostomatales* and *Microstromatales*. All available published sequence data were screened for reliable sequences representing as many species as possible, and new data were generated where necessary for ex-type or other isolates. The resulting phylogenies enabled the formal redefinition of the *Ophiostomatales* and *Ophiostomataceae*, and the description of two new families, the *Graphiaceae* (*Microascales*) and *Quambalariaceae* (*Microstromatales*). Problems relating to the delineation of *Ophiostoma s.l.*, *Leptographium s.l.*, and *Raffaelea s.l.* were exposed and discussed, 18 species complexes were defined in the *Ophiostomatales*, and four genera were formally redefined: *Sporothrix*, *Graphium*, *Graphilbum* and *Knoxdaviesia*. Forty six new combinations were made, primarily in *Sporothrix*, *Ophiostoma*, *Graphilbum* and *Knoxdaviesia*. One *nomen novum* was erected in *Ceratocystis* and one new *Quambalaria* species was described. A comprehensive nomenclator for 596 ophiostomatoid species including references to all descriptions, synonymies and phylogenetic data was also compiled. This study represents the first comprehensive, all-inclusive assessment of the taxonomy and nomenclature of the ophisotomatoid fungi based on phylogenetic relationships and the one fungus one name principles. Finally, the immediate and indiscriminate application of the one fungus one name principles in *Ophiostoma s.l.* and *Leptographium s.l.* might result in many unnecessary name changes. Thus, several recommendations have been made to ensure nomenclatural stability in these genera in the immediate future and until more robust phylogenies become available that can refine the delineation of these genera.

Key words
Microascales, *Microstromatales*, nomenclature, one fungus one name, *Ophiostomatales*, ophiostomatoid fungi, *Quambalaria, Sporothrix schenckii*, taxonomy