

Redefining *Ceratocystis* and allied genera

Z.W. de Beer^{1,3}, T.A. Duong^{2,3}, I. Barnes², B.D. Wingfield², and M.J. Wingfield¹

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

*Correspondence: Z.W. de Beer. wilhelm.debeer@fabi.up.ac.za

³These authors contributed equally to this study.

Abstract: The genus *Ceratocystis* was established in 1890 and accommodates many important fungi. These include serious plant pathogens, significant insect symbionts and agents of timber degradation that result in substantial economic losses. Virtually since its type was described from sweet potatoes, the taxonomy of *Ceratocystis* has been confused and vigorously debated. In recent years, particularly during the last two decades, it has become very obvious that this genus includes a wide diversity of very different fungi. These have been roughly lumped together due to their similar morphological structures that have clearly evolved through convergent evolution linked to an insect-associated ecology. As has been true for many other groups of fungi, the emergence of DNA-based sequence data and associated phylogenetic inferences, have made it possible to robustly support very distinct boundaries defined by morphological characters and ecological differences. In this study, DNA-sequence data for three carefully selected gene regions (60S, LSU, MCM7) were generated for 79 species residing in the aggregate genus *Ceratocystis sensu lato* and these data were subjected to rigorous phylogenetic analyses. The results made it possible to distinguish seven major groups for which generic names have been chosen and descriptions either provided or emended. The emended genera included *Ceratocystis sensu stricto*, *Chalaropsis*, *Endoconidiophora*, *Thielaviopsis*, and *Ambrosiella*, while two new genera, *Davidsoniella* and *Huntiella*, were described. In total, 30 new combinations have been made. This major revision of the generic boundaries in the *Ceratocystidaceae* will simplify future treatments and work with an important group of fungi including distantly related species illogically aggregated under a single name.

Key words: *Ceratocystidaceae*, New combinations, Nomenclature, Multigene analyses, Taxonomy.

Taxonomic novelties: New genera: *Davidsoniella* Z.W. de Beer, T.A. Duong & M.J. Wingf., *Huntiella* Z.W. de Beer, T.A. Duong & M.J. Wingf; **New combinations:** *Chalaropsis ovoidea* (Nag Raj & W.B. Kendr.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *Ch. populi* (Kiffer & Delon) Z.W. de Beer, T.A. Duong & M.J. Wingf., *Davidsoniella australis* (J. Walker & Kile) Z.W. de Beer, T.A. Duong & M.J. Wingf., *D. eucalypti* (Z.Q. Yuan & Kile) Z.W. de Beer, T.A. Duong & M.J. Wingf., *D. neocaledoniae* (Kiffer & Delon) Z.W. de Beer, T.A. Duong & M.J. Wingf., *D. virescens* (R.W. Davidson) Z.W. de Beer, T.A. Duong & M.J. Wingf., *Endoconidiophora douglasii* (R.W. Davidson) Z.W. de Beer, T.A. Duong & M.J. Wingf., *E. fujiensis* (M.J. Wingf., Yamaoka & Marin) Z.W. de Beer, T.A. Duong & M.J. Wingf., *E. laricicola* (Redfern & Minter) Z.W. de Beer, T.A. Duong & M.J. Wingf., *E. pinicola* (T.C. Harr. & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *E. polonica* (Siemaszko) Z.W. de Beer, T.A. Duong & M.J. Wingf., *E. resinifera* (T.C. Harr. & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *E. rufipennis* (M.J. Wingf., T.C. Harr. & H. Solheim) Z.W. de Beer, T.A. Duong & M.J. Wingf., *Huntiella bhutanensis* (M. van Wyk, M.J. Wingf. & T. Kirisits) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. ceramica* (R.N. Heath & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. chinaeucensis* (S.F. Chen, M. van Wyk, M.J. Wingf. & X.D. Zhou) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. cryptoformis* (Mbenoun & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. decipiens* (Kamgan & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. inquinans* (Tarigan, M. van Wyk & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. microbasis* (Tarigan, M. van Wyk & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. moniliformis* (Hedgc.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. moniliformopsis* (Yuan & Mohammed) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. oblonga* (R.N. Heath & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. omanensis* (Al-Subhi, M.J. Wingf., M. van Wyk & Deadman), Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. salinaria* (Kamgan & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. savannae* (Kamgan & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. sublaevis* (M. van Wyk & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. sumatrana* (Tarigan, M. van Wyk & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. tribiliformis* (M. van Wyk & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., *H. tyalla* (Kamgan & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., *Thielaviopsis cerberus* (Mbenoun, M.J. Wingf. & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf.

Published online 7 November 2014; <http://dx.doi.org/10.1016/j.simyco.2014.10.001>. Hard copy: September 2014.

INTRODUCTION

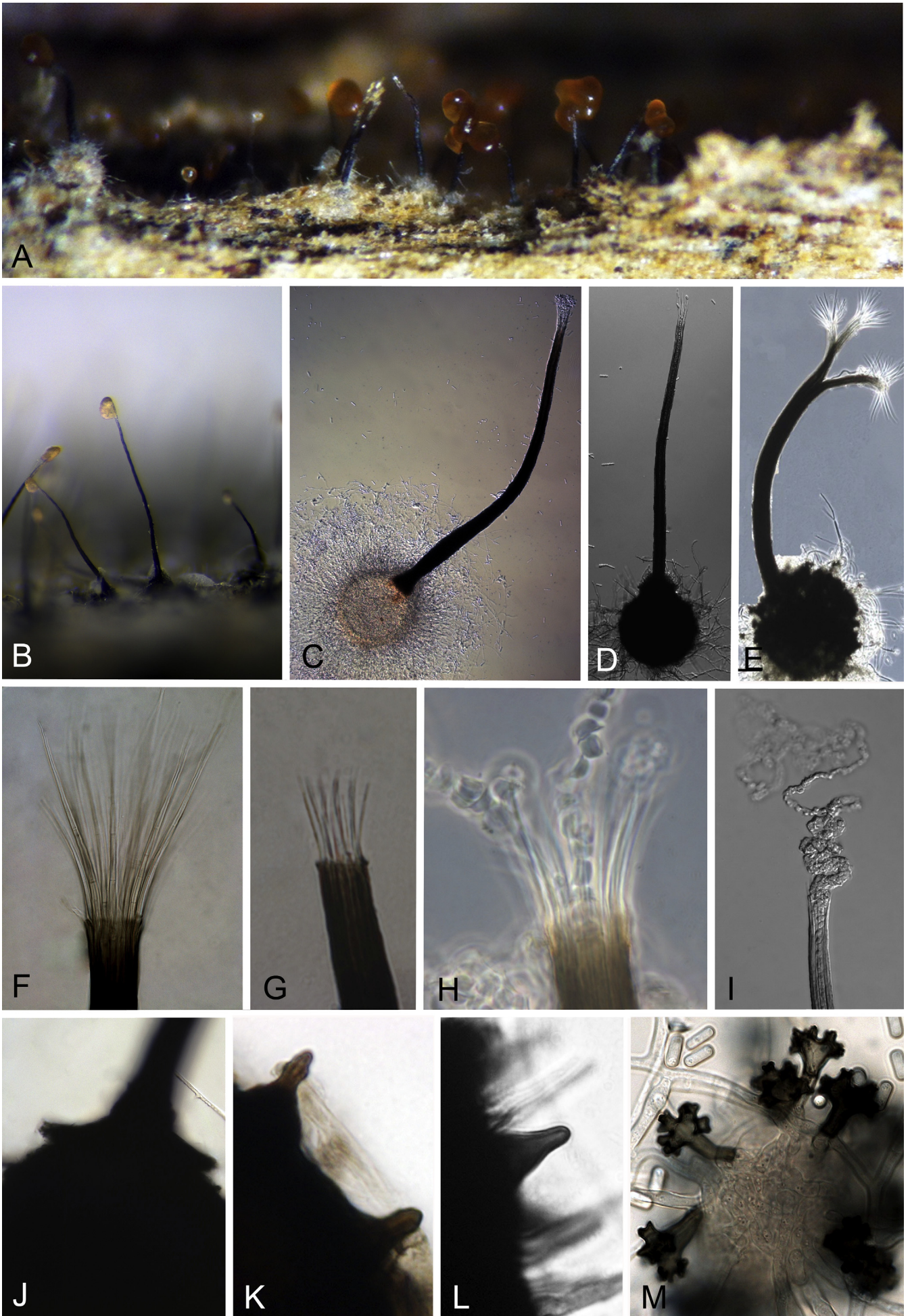
Ceratocystis was established in 1890 to accommodate *C. fimbriata*, a pathogen causing black rot of sweet potatoes in the USA (Halsted 1890). The genus now includes many important fungi including important pathogens of plants and the causal agents of sap stain in timber that are symbiotic associates of insects (Fig. 1). These fungi have ascospores with round usually dark bases that are sometimes ornamented. These bases give rise to long necks terminating in ostiolar hyphae and from which ascospores exude in slimy masses (Fig. 2). All species have ascospores surrounded by sheaths, which can be hat-shaped, ellipsoidal or obovoid and that are either evenly or unevenly distributed around the spores (Fig. 3). The asexual states of most

species in *Ceratocystis* are morphologically “chalara”- or “thielaviopsis”-like forms and characterised by simple, tubular conidiogenous cells. These cells, which are phialides, typically taper towards their apices and produce chains of rectangular conidia or in some cases dark barrel-shaped secondary conidia (Fig. 3). Some species produce simple, single-celled or more complex chlamydo-spores (Fig. 3) that facilitate a soil-borne life-style.

Since the time of its first discovery, *Ceratocystis* has been beset by taxonomic complications and controversy. The first of these emerged with the description of *Ophiostoma* in 1919 (Sydow & Sydow 1919). It was set up to accommodate several *Ceratostomella* spp., with *O. piliferum* as type species and including *Ceratostomella moniliformis*. Not long thereafter, Melin & Nannfeldt (1934) disposed additional species in the genus,



Fig. 1. Disease symptoms of plants infected with species of *Ceratocystis* s.l. A. Eucalyptus wilt in Uruguay caused by *C. fimbriata* s.l. B. Dying clove trees infected with *C. polychroma* in Sulawesi. C. Wilting shoots of *Acacia meamsii* in South Africa infected with *C. albifundus*. D. *Ceratocystis* wilt of *Acacia* sp. caused by *C. manginecans*. E, F. Wilted shoots and damaged stems of *Protea cynaroides* in South Africa caused by *C. albifundus*. G. Resin exudation from the stem of *A. meamsii* in South Africa caused by *C. albifundus*. H. Fungal mats of *C. albifundus* on *Acacia exuvialis*. I. Vascular streaking caused by *C. manginecans* after wounding. J. Fungal mats of *C. albifundus* on *A. exuvialis*. K. Staining of the wood of *Acacia* caused by *C. albifundus*. L. Streaking and stain of mango trees from infections by *C. manginecans* in Oman. M. Cross section through a *Eucalyptus grandis* stump showing streaking caused by *C. fimbriata* s.l. N. Sweet potato with black rot caused by *C. fimbriata* s. str. O. Rotted cacao pod infected with *C. ethacetica* (now *T. ethacetica*). P. Ascomata of *C. polonica* (now *E. polonica*) in the gallery of the bark beetle *Ips typographus*.



including the type species of *Ceratocystis*, *C. fimbriata*. These studies and others (Bakshi 1951, Moreau 1952) resulted in a long-standing confusion between the two genera. This is largely because the genera have morphologically similar ascomata featuring globose bases and generally long necks from which ascospores exude in slimy masses (Upadhyay 1981). According to Malloch & Blackwell (1993) the basic construction of the ascomata may be the result of an adaptation to insect-associated niches and shows the convergent evolution of fruiting structures that facilitate insect-borne transport of spores to new environments (Malloch & Blackwell 1993). Interestingly, but adding to the confusion between them, species of both *Ceratocystis* and *Ophiostoma* have evanescent asci that are seldom seen. Ascospores were confused with conidia when the genera were first discovered. The fact that both genera include species with hat-shaped ascospores re-inforced debate over their relationships for many years (Van Wyk et al. 1993).

The taxonomic confusion between *Ceratocystis* and *Ophiostoma* was finally resolved once DNA sequence data became available to provide phylogenetic insights into their relatedness. Hausner et al. (1993a,b) and Spatafora & Blackwell (1994) provided the first phylogenetic trees showing that these genera are unrelated. A considerable body of evidence has contributed to the current understanding that *Ophiostoma* resides in the *Ophiostomatales* in the *Sordariomycetidae* and that *Ceratocystis* is accommodated in the *Ceratocystidaceae* (*Microascales*) in the *Hypocreomycetidae* (Réblová et al. 2011, De Beer et al. 2013a). Importantly, resolution of the taxonomic confusion regarding these genera has made it possible to study them independently and thus to better understand their similarities, but also their many very different ecologies (Seifert et al. 2013).

Once *Ceratocystis* was clearly recognised as unrelated to *Ophiostoma*, an increasingly clear picture emerged of a genus that included species that were morphologically and ecologically very distinct from one another. These differences have been substantially amplified by the discovery of many new and often cryptic species, revealed through DNA-sequence comparisons (Wingfield et al. 1996, Witthuhn et al. 1998, Harrington & Wingfield 1998). For example, perhaps the two best-known species names within *Ceratocystis*, *C. fimbriata* and *C. moniliformis*, are now known to represent complexes of many different species (Van Wyk et al. 2013, Wingfield et al. 2013). Recognition of these complexes has made it possible to interpret their very clear differences.

Wingfield et al. (2013) provided the first intensive, phylogenetically based reconsideration of the taxonomy of *Ceratocystis*. This study included all available sequence data up to 2006 when the study was completed, and it clearly exposed five very different taxonomic groups. These included the species of the *C. fimbriata* complex, the *C. moniliformis* complex, and the *C. coerulescens* complex, as well the *Thielaviopsis* and *Ambrosiella* complexes, known only by their asexual states. Importantly, species in these complexes could easily be separated by their morphological and ecological differences. The DNA sequence data used merely

reaffirmed the circumscription of the groups. Wingfield et al. (2013) provided substantial evidence that species in *Ceratocystis* s. l. should be assigned to discrete genera. They argued that this would substantially reduce taxonomic confusion among these very different groups of fungi and importantly, also enhance understanding of their different ecologies.

Wingfield et al. (2013) were not able to place all species of *Ceratocystis* s. l. in discrete complexes. Some, such as *C. paradoxa*, *C. adiposa* and *C. fagacearum* fell away from all clearly defined species groups. In retrospect, it appears that this problem stemmed from a lack of sampling and was resolved by the discovery of additional species that could define complexes based on these isolated phylogenetic branches. Such a pattern has become clearly evident from a recent study of a large collection of isolates that would previously have been identified as *C. paradoxa* (Mbenoun et al. 2014a). These isolates have now been shown to represent a number of very different but related species that are now recognised as comprising the *C. paradoxa* complex. It is, therefore, very likely that other complexes will emerge in *Ceratocystis* s. l., as new species are collected and treated in the future.

Ceratocystis s. l., as it is currently defined includes many ecologically important fungi (Fig. 1). For example, most species in the *C. fimbriata* complex are important and in some cases devastating plant pathogens (Kile 1993, Wingfield et al. 2013). These include *C. albifundus*, a virulent pathogen of *Acacia mearnsii* in Africa (Roux & Wingfield 2013), *C. cacaofunesta*, a pathogen of cacao in South America (Engelbrecht et al. 2007), *C. platani*, an invasive alien pathogen of *Platanus* trees in Europe (Gibbs 1981, Ocasio-Morales et al. 2007), and *C. manginecans* that has devastated mango (*Mangifera indica*) and *Acacia mangium* trees in the Middle East and south-east Asia respectively (Van Wyk et al. 2007, Tarigan et al. 2011).

Species in the *C. coerulescens* complex include associates of bark beetles (Coleoptera: Scolytinae) as well as important causal agents of sap-stain in timber (Seifert 1993, Wingfield et al. 1997). The *Thielaviopsis* complex includes plant pathogens, while the *Ambrosiella* complex comprise obligate associates of ambrosia beetles (Coleoptera: Scolytinae) (Batra 1967, Kile 1993). Species in the *C. moniliformis* complex are mostly wound-inhabiting saprobes or mild pathogens, often causing sap stain in timber (Hedgcock 1906, Seifert 1993). The members of the *C. paradoxa* complex are all pathogens of monocotyledonous plants, including pineapples and palms (Mitchell 1937, Alvarez et al. 2012, Mbenoun et al. 2014a).

All available evidence shows that *Ceratocystis* s. l. represents a suite of morphologically, phylogenetically and ecologically different fungi. There is no reasonable argument for retaining them in a unitary genus, and indeed, doing so would result only in confusion arising from a diminished lack of appreciation of their dramatic differences. Placing them in discrete genera will enhance the perception of opportunities to understand these organisms and, where applicable, to manage or conserve them. It will provide an improved interpretive framework for analysing

Fig. 2. Morphological features of the ascomata of species of *Ceratocystis* s.l. A, B. Ascomata of *C. albifundus* and *C. fimbriata* respectively, on woody substrates with masses of ascospores emerging from their necks. C–E. Ascomata showing different morphological features such as light-coloured bases of *C. albifundus* (CMW4059), pear-shaped ascomatal bases characteristic of *C. pirilliformis* (CMW6579), ornamented bases and divergent necks of *C. cerberus* (now *T. cerberus*) (CMW 36668). F, G. Apices of ascomata showing a range of forms of ostiolar hyphae such as long, divergent ostiolar hyphae of *C. ethacetica* (CMW 36671) (now *T. ethacetica*) and short, convergent ostiolar hyphae of *C. inquinans* (now *H. inquinans*) (CMW 21106). H, I. Hat-shaped ascospores being released from ostiolar hyphae in *C. sumatrana* (now *H. sumatrana*) (CMW 21113) and *C. pirilliformis* (CMW 6670). J. Bases of ascomata in the *C. moniliformis* s.l. complex (now *Huntliella*) with distinct plates at the bases of the ascomatal necks, and (K, L) spine-like ornamentations of *H. microbasis* (CMW 21117) and *H. oblonga* (CMW 23803) respectively. M. Digitate ornamentations on the ascomatal bases in species residing in *C. paradoxa* s.l. (now *Thielaviopsis*) (CMW 36642).



Fig. 3. Sexual and asexual spores in *Ceratocystis* s.l. A–D. A range of ascospore shapes all with hyaline sheaths and including those that are fusoid [e.g. *C. eucalypti* (now *D. eucalypti*), photo from Kile *et al.* 1996], hat-shaped (e.g. *C. fimbriata*, CMW 15049), oblong (e.g. *C. paradoxa*, now *T. paradoxa*, CMW 36642) and obovoid (e.g. *C. laricicola*, now *E. laricicola*, CMW 20928). E–H. Simple tubular conidiophores commonly tapering to their apices, and found in most species of *Ceratocystis* s.l. E. Flasked-shaped phialidic conidiophores of *T. paradoxa* (CMW 36642) releasing obovoid secondary conidia. F. Phialide releasing cylindrical conidia of *C. pirilliformis* (CMW 6670). G. Chlamydospore of *T. basicola* (CMW 7068) and H. *C. pirilliformis* (CMW 6670). I–L. Darkly pigmented, thick-walled aleurioconidia of (I) *T. paradoxa* (CMW 36642), (J) *T. euricoi* (CMW 28537), (K) *T. punctulata* (CMW 26389) and (L) *T. ethacetica* (CMW 36671). M, N. Cylindrical and barrel-shaped conidia of *C. pirilliformis* (CMW 6670). O. Oblong secondary conidia of *T. ethacetica* (CMW 36671). P. Secondary conidia of *T. punctulata* (CMW 26389).

the ecological differences among the species, such as differences in pathogenicity and insect associations, particularly when complete genome sequences become available for these fungi, as they have recently done for *C. fimbriata* s. str., *C. moniliformis* s. str. and *C. manginecans* (Wilken et al. 2013, Van der Nest et al. 2014).

Revising *Ceratocystis* s. l. and providing genera to accommodate the well-defined groups in this aggregate genus must be done in conformity with the principles of the new International Code for algae, fungi and plants (Melbourne Code) adopted at the 18th International Botanical Congress (McNeill et al. 2012). Importantly, this must reflect the One Fungus One Name (1F1N) principles that originally emerged from the Amsterdam Declaration (Hawksworth et al. 2011) and subsequent discussions (Hawksworth 2011, Norvell 2011, Wingfield et al. 2012). In this regard, De Beer et al. (2013b) listed six genus names as possible synonyms of *Ceratocystis* s. l. One of these names belongs to a sexual genus *Endoconidiophora*, originally described for *E. coeruleascens* (Münch 1907). The five other names were all considered to denote asexual genera under the dual nomenclature system: they included *Thielaviopsis* (Went 1893, type species *T. ethacetica*), *Chalaropsis* (Peyronel 1916, type species *Ch. thielavioides*), *Hughesiella* (Batista & Vital 1956, type species *Hu. euricoi*), *Ambrosiella* (Von Arx & Hennebert 1965, type species *A. xylebori*), and *Phialophoropsis* (Batra 1967, type species *Ph. trypodendri*). These names are available for new generic circumscriptions accommodating groups currently residing in *Ceratocystis* s. l.

The major aim of this study was to revise the generic boundaries for species currently accommodated in *Ceratocystis* s. l. This task involved obtaining material from as many species as possible and applying 1F1N principles. Generating the full genome sequences for 19 species including representatives of all the phylogenetic groups in *Ceratocystis* s. l. provided the opportunity to screen multiple gene regions to address genus-level questions. In addition, gene regions from the AFTOL project (Lutzoni et al. 2004, Hibbett et al. 2007), the ITS barcoding initiative (Schoch et al. 2012), as well as additional barcoding genes from an ongoing project at CBS (Stielow et al. 2014) were used to design *Microascales*-specific primers and to select the most appropriate gene regions to clearly resolve generic boundaries for *Ceratocystis* s. l.

MATERIALS AND METHODS

Cultures

All cultures used in this study were obtained from the Culture Collection of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa (CMW) and Centraalbureau voor Schimmelcultures, Utrecht, the Netherlands (CBS). Single spore or single hyphal-tip cultures were prepared and maintained on 2 % Malt Extract Agar (MEA). A list of isolates used in this study is presented in Table 1.

DNA extraction

Single spore/single hyphal-tip cultures were inoculated in YM broth (2 % malt extract, 0.2 % yeast extract) and incubated at 25 °C with shaking for 2–5 d. Mycelium was harvested and

freeze-dried in 2 mL Eppendorf tubes. The freeze-dried mycelium was submerged in liquid nitrogen, followed by pulverising the mycelium with a pipette tip. About 10 mg of mycelial “powder” was used for DNA extraction using PrepMan Ultra Sample Preparation reagent (Applied Biosystems, Foster City, California) as described in Duong et al. (2012).

Selection of gene regions and primers

Ten different gene regions [the nuclear ribosomal DNA large subunit (LSU), the nuclear ribosomal DNA small subunit (SSU), nuclear ribosomal DNA internal transcribed spacer regions (ITS), the 60S ribosomal protein RPL10 (60S), beta-tubulin (BT), translation elongation factor 1-alpha (EF1), translation elongation factor 3-alpha (EF3), mini-chromosome maintenance complex component 7 (MCM7), the RNA polymerase II largest subunit (RPB1), and the RNA polymerase II second largest subunit (RPB2)] were extracted from 19 *Ceratocystis* draft genome sequences that included species from all the major clades. The genome sequences, of which three have been published (Wilken et al. 2013, Van der Nest et al. 2014), are available at the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria. Phylogenetic analyses were conducted with all ten gene regions (data not shown). LSU, 60S, and MCM7 were selected as candidate genes for further investigation including all the isolates in the study, based on their level of support at the basal nodes, the ease of amplification and sequencing, and the popularity of their use in studies of other fungal lineages.

The ITS region has been widely used in phylogenetic studies to distinguish between species in *Ceratocystis*. However, due to the recent discovery of multiple ITS forms in certain species of *Ceratocystis* (Al Adawi et al. 2013, Naidoo et al. 2013), and the fact that gene regions were chosen that were slightly more conserved to resolve the genus level questions, the ITS was intentionally not used in the present study.

Primers LR0R and LR5 (Vilgalys & Hester, 1990) were used in PCR amplification and sequencing of LSU. Primers Algr52_412-433_f1 and Algr52_1102_1084_r1 (Stielow et al. 2014) were used for PCR amplification and sequencing of 60S. Based on the sequences obtained from genomes, new primers Cer-MCM7F (ACICGIGTITCIGAYGTNAAGCC) and Cer-MCM7R (TTRGCAACACCAGRTCACCCAT) were designed and used in PCR amplification and sequencing of MCM7.

PCR and sequencing

All PCR reactions were done in a total volume of 25 µL. The reaction mixture consisted of 2.5 µL of 10X PCR reaction buffer, 2.5 mM MgCl₂, 200 µM of each dNTP, 0.2 µM of each of the forward and reverse primers for LSU (1 µM of each primer in case of degenerate primers for 60S and MCM7), 1 U FastStart Taq DNA Polymerase (Roche) and 2 µL of genomic DNA solution. The PCR thermal conditions included an initial denaturation at 96 °C for 5 min, followed by 35 cycles of 95 °C for 30 sec, 55 °C for 30 s, and 72 °C for 60 s, and ended with a final extension at 72 °C for 8 min. The annealing temperature was set at 55 °C for all gene regions and all isolates at first. In some cases where the PCR failed or non-specific amplification was observed, we experimented with different annealing

Table 1. Isolates used in the phylogenetic analyses in this study.

Previous name	New name	Country	Host/substrate	Collector; collection year	Herbarium Specimen ¹	Culture collection number(s) ¹	Strain status	GenBank accession numbers ²		
								60S	LSU	MCM7
<i>Ambrosiella beaveri</i>	<i>Ambrosiella beaveri</i>	USA	<i>Vitis rotundifolia</i>	D. Six; 2005	–	CMW 26179; CBS 121753; DLS 1624	ex-paratype	KM495492	KM495315	KM495405
<i>A. ferruginea</i>	<i>A. ferruginea</i>	Germany	<i>Fagus sylvatica</i>	G. Zimmerman; 1971	–	CMW 25522; CBS 460.82	not type	KM495493	KM495316	KM495406
<i>A. hartigii</i>	<i>A. hartigii</i>	Germany	<i>Acer</i> sp.	– ; 1970	–	CMW 25525; CBS 403.82	not type	KM495494	KM495317	–
<i>A. xylebori</i>	<i>A. xylebori</i>	Ivory Coast	<i>Coffea canephora</i>	L. Brader; 1961	–	CMW 25531; CBS 110.61	ex-isotype	KM495495	KM495318	KM495407
<i>Ceratocystis acaciivora</i>	<i>Ceratocystis acaciivora</i>	Indonesia	<i>Acacia mangium</i>	M. Tarigan; 2005	PREM 59884	CMW 22563	ex-holotype	KM495496	KM495319	KM495408
<i>C. adiposa</i>	<i>C. adiposa</i>	Japan	<i>Saccharum officinarum</i>	T. Miyake; 1934	–	CMW 2573; CBS 136.34	not type	KM495497	KM495320	KM495409
<i>C. albifundus</i>	<i>C. albifundus</i>	South Africa	<i>Acacia mearnsii</i>	J. Roux; 1997	–	CMW 4068; CBS 128992	not type	KM495498	KM495321	KM495410
<i>C. atrox</i>	<i>C. atrox</i>	Australia	<i>Eucalyptus grandis</i>	M.J. Wingfield; 2005	PREM 59012	CMW 19385; CBS 120518	ex-holotype	KM495499	KM495322	KM495411
<i>C. bhutanensis</i>	<i>Huntia bhutanensis</i>	Bhutan	<i>Picea spinulosa</i>	T. Kirisits & D.B. Chhetri; 2001	PREM 57804	CMW 8217; CBS 114289	ex-holotype	KM495500	KM495323	KM495412
<i>C. cacaofunesta</i>	<i>C. cacaofunesta</i>	Ecuador	<i>Theobromae cacao</i>	T.C. Harrington; 2000	BPI 843731	CMW 14803; CBS 115163; C 1695	original collection	KM495501	KM495324	KM495413
<i>C. caryae</i>	<i>C. caryae</i>	USA	<i>Carya ovata</i>	J.A. Johnson; 2001	–	CMW 14808; CBS 115168; C 1827	original collection	KM495502	KM495325	KM495414
<i>C. cerberus</i>	<i>Thielaviopsis cerberus</i>	Cameroon	<i>Elaeis guineensis</i>	M. Mbenoun & J. Roux; 2010	PREM 60770	CMW 36668; CBS 130765	ex-holotype	KM495503	KM495326	KM495415
<i>C. chinaeucensis</i>	<i>H. chinaeucensis</i>	China	<i>Eucalyptus grandis</i> x <i>E. urophylla</i>	M.J. Wingfield & S.F. Chen; 2006	PREM 60735	CMW 24658; CBS 127185	ex-holotype	KM495504	KM495327	KM495416
<i>C. coerulescens</i>	<i>Endoconidiophora coerulescens</i>	Germany	<i>Picea abies</i>	T. Rohde; 1937	–	CMW 26365; CBS 140.37; MUCL 9511; C 313; C 695	not type	KM495506	KM495329	KM495418
<i>C. colombiana</i>	<i>C. colombiana</i>	Colombia	<i>Coffea arabica</i>	M. Marin; 2000	PREM 59434	CMW 5751; CBS 121792	ex-holotype	KM495507	KM495330	KM495419
<i>C. corymbicola</i>	<i>C. corymbicola</i>	Australia	<i>Eucalyptus pilularis</i>	G. Kamgan Nkuekam; 2008	PREM 60433	CMW 29349; CBS 127216	ex-paratype	KM495508	KM495331	KM495420
<i>C. curvata</i>	<i>C. curvata</i>	Ecuador	<i>Eucalyptus deglupta</i>	M.J. Wingfield; 2004	PREM 60154	CMW 22432	ex-paratype	KM495509	KM495332	KM495421
<i>C. decipiens</i>	<i>H. decipiens</i>	South Africa	<i>Eucalyptus saligna</i>	G. Kamgan Nkuekam & J. Roux; 2008	PREM 60560	CMW 30855; CBS 129736	ex-holotype	KM495510	KM495333	KM495422
<i>C. diversiconidia</i>	<i>C. diversiconidia</i>	Ecuador	<i>Terminalia ivorensis</i>	M.J. Wingfield; 2004	PREM 60160	CMW 22445; CBS 123013	ex-holotype	KM495511	KM495334	KM495423
<i>C. douglasii</i>	<i>E. douglasii</i>	USA	<i>Pseudotsuga taxifolia</i>	R.W. Davidson; 1951	BPI 595613 = FP 70703	CMW 26367; CBS 556.97	ex-holotype	KM495512	KM495335	KM495424
<i>C. ecuadoriana</i>	<i>C. ecuadoriana</i>	Ecuador	<i>Eucalyptus deglupta</i>	M.J. Wingfield; 2004	PREM 60155	CMW 22092; CBS 124020	ex-holotype	KM495513	KM495336	KM495425
<i>C. ethacetica</i>	<i>T. ethacetica</i>	Malaysia	<i>Ananas comosus</i>	A. Johnson; 1952	PREM 60961	CMW 37775; IMI 50560; MUCL 2170	ex-epitype	KM495514	KM495337	KM495426

(continued on next page)

Table 1. (Continued)

Previous name	New name	Country	Host/substrate	Collector; collection year	Herbarium Specimen ¹	Culture collection number(s) ¹	Strain status	GenBank accession numbers ²		
								60S	LSU	MCM7
<i>C. eucalypti</i>	<i>Davidsoniella eucalypti</i>	Australia	<i>Eucalyptus sieberi</i>	M.J. Dudzinski; 1989	DAR 70205	CMW 3254; C 639	ex-holotype	KM495515	KM495338	KM495427
<i>C. eucalypticola</i>	<i>C. eucalypticola</i>	South Africa	<i>Eucalyptus</i> sp.	M. van Wyk & J. Roux; 2002	PREM 60168	CMW 11536; CBS 124016	ex-holotype	KM495516	KM495339	KM495428
<i>C. fagacearum</i>	<i>C. fagacearum</i>	USA	<i>Quercus rubra</i>	S. Seegmuller; 1991	–	CMW 2656; C463	not type	KM495518	KM495341	KM495430
<i>C. ficicola</i>	<i>C. ficicola</i>	Japan	<i>Ficus carica</i>	Y. Kajitani; 1990	NIAES 20600	CMW 38543; MAFF 625119	ex-holotype	KM495519	KM495342	KM495431
<i>C. fimbriata</i>	<i>C. fimbriata</i>	USA	<i>Ipomoea batatas</i>	C.F. Andrus; 1937	–	CMW 15049; CBS 141.37	not type	KM495520	KM495343	KM495432
<i>C. fimbriatomima</i>	<i>C. fimbriatomima</i>	Venezuela	<i>Eucalyptus</i> hybrid	M.J. Wingfield; 2006	PREM 59439	CMW 24174; CBS 121786	ex-holotype	KM495521	KM495344	KM495433
<i>C. fujiensis</i>	<i>E. fujiensis</i>	Japan	<i>Larix kaempferi</i>	M.J. Wingfield & Y. Yamaoka; 1997	PREM 57513	CMW 1955; CBS 100208; JCM 9810	ex-holotype	KM495522	KM495345	KM495434
<i>C. harringtonii</i> (= <i>C. populicola</i>)	<i>C. harringtonii</i>	Netherlands	<i>Populus</i> hybrid	J. Gremmen; 1978	–	CMW 14789; CBS 119.78; C 995	original collection	KM495523	KM495346	KM495435
<i>C. inquinans</i>	<i>H. inquinans</i>	Indonesia	<i>Acacia mangium</i>	M. Tarigan; 2005	PREM 59866	CMW 21106; CBS 124388	ex-holotype	KM495524	KM495347	KM495436
<i>C. laricicola</i>	<i>E. laricicola</i>	UK	<i>Larix decidua</i>	D. Redfern; 1983	–	CMW 20928; CBS 100207; C 181; Redfern 56-10	ex-paratype	KM495525	KM495348	KM495437
<i>C. larium</i>	<i>C. larium</i>	Indonesia	<i>Styrax benzoin</i>	M.J. Wingfield; 2007	PREM 60193	CMW 25434; CBS 122512	ex-holotype	KM495526	KM495349	–
<i>C. major</i>	<i>C. adiposa</i>	Netherlands	Air	F.H. van Beyma; 1934	–	CMW 3189; CBS 138.34; ATCC 11932; MUCL 9518	ex-holotype	KM495527	KM495350	KM495438
<i>C. mangicola</i>	<i>C. mangicola</i>	Brazil	<i>Mangifera indica</i>	C.J. Rosetto; 2008	PREM 60185	CMW 28908; CBS 127210	ex-paratype	KM495528	KM495351	KM495439
<i>C. manginecans</i>	<i>C. manginecans</i>	Oman	<i>Prosopis cineraria</i>	A. Al Adawi; 2005	–	CMW 17570; CBS 138185	not type	KM495529	KM495352	KM495440
<i>C. mangivora</i>	<i>C. mangivora</i>	Brazil	<i>Mangifera indica</i>	C.J. Rosetto; 2001	PREM 60570	CMW 27305; CBS 128702	ex-holotype	KM495530	KM495353	KM495441
<i>C. microbasis</i>	<i>H. microbasis</i>	Indonesia	<i>Acacia mangium</i>	M. Tarigan; 2005	PREM 59872	CMW 21117	ex-holotype	KM495531	KM495354	KM495442
<i>C. moniliformis</i>	<i>H. moniliformis</i>	South Africa	<i>Eucalyptus grandis</i>	M. van Wyk; 2002	–	CMW 10134; CBS 118127	not type	KM495532	KM495355	KM495443
<i>C. moniliformopsis</i>	<i>H. moniliformopsis</i>	Australia	<i>Eucalyptus obliqua</i>	Z.Q. Yuan; 2001	DAR 74608	CMW 9986; CBS 109441	ex-holotype	KM495533	KM495356	KM495444
<i>C. musarum</i>	<i>T. musarum</i>	New Zealand	<i>Musa</i> sp.	T.W. Canter-Visscher; –	PREM 60962	CMW 1546; C 907	ex-epitype	KM495534	KM495357	KM495445
<i>C. neglecta</i>	<i>C. neglecta</i>	Colombia	<i>Eucalyptus grandis</i>	C. Rodas & J. Roux; 2004	PREM 59616	CMW 17808; CBS 121789	ex-holotype	KM495535	KM495358	KM495446
<i>C. oblonga</i>	<i>H. oblonga</i>	South Africa	<i>Acacia mearnsii</i>	R.N. Heath; 2006	PREM 59792	CMW 23803; CBS 122291	ex-holotype	KM495536	KM495359	KM495447
<i>C. obpyriformis</i>	<i>C. obpyriformis</i>	South Africa	<i>Acacia mearnsii</i>	R.N. Heath; 2006	PREM 59796	CMW 23808; CBS 122511	ex-holotype	KM495537	KM495360	KM495448
<i>C. omanensis</i>	<i>H. omanensis</i>	Oman	<i>Mangifera indica</i>	A. Al Adawi & M. Deadman; 2003	–	CMW 11056; CBS 118113	original collection	KM495538	KM495361	KM495449
<i>C. papillata</i>	<i>C. papillata</i>	Colombia	<i>Citrus</i> x Tangelo hybrid	B. Castro; 2001	PREM 59438	CMW 8856; CBS 121793	ex-holotype	KM495539	KM495362	KM495450

(continued on next page)

Table 1. (Continued)

Previous name	New name	Country	Host/substrate	Collector; collection year	Herbarium Specimen ¹	Culture collection number(s) ¹	Strain status	GenBank accession numbers ²		
								60S	LSU	MCM7
<i>C. paradoxa</i>	<i>T. paradoxa</i>	Cameroon	<i>Theobromae cacao</i>	M. Mbenoun & J. Roux; 2010	PREM 60766	CMW 36689; CBS 130761	ex-epitype	KM495540	KM495363	KM495451
<i>C. pinicola</i>	<i>E. pinicola</i>	UK	<i>Pinus sylvestris</i>	J. Gibbs; 1988	DAOM 225447	CMW 29499; CBS 100199; C 488; DAOM 225447	ex-holotype	KM495541	KM495364	KM495452
<i>C. pirilliformis</i>	<i>C. pirilliformis</i>	Australia	<i>Eucalyptus nitens</i>	M.J. Wingfield; 2000	PREM 57323	CMW 6579; CBS 118128	ex-holotype	KM495542	KM495365	KM495453
<i>C. platani</i>	<i>C. platani</i>	USA	<i>Platanus occidentalis</i>	T.C. Harrington; 1998	–	CMW 14802; CBS 115162; C 1317	original collection	KM495543	KM495366	KM495454
<i>C. polonica</i>	<i>E. polonica</i>	Norway	<i>Picea abies</i>	H. Solheim; 1990	DAOM 225451	CMW 20930; CBS 100205; C791	ex-neotype	KM495544	KM495367	KM495455
<i>C. polychroma</i>	<i>C. polychroma</i>	Indonesia	<i>Syzygium aromaticum</i>	E.C.Y. Liew; 2002	PREM 57818	CMW 11424; CBS 115778	ex-holotype	KM495545	KM495368	KM495456
<i>C. polyconidia</i>	<i>C. polyconidia</i>	South Africa	<i>Acacia mearnsii</i>	R.N. Heath; 2006	PREM 59788	CMW 23809; CBS 122289	ex-holotype	KM495546	KM495369	KM495457
<i>C. radicolata</i>	<i>T. punctulata</i>	USA	<i>Phoenix dactylifera</i>	D.E. Bliss; –	BPI 596268	CMW 1032; CBS 114.47; MUCL 9526	ex-holotype	KM495548	KM495371	KM495459
<i>C. resinifera</i>	<i>E. resinifera</i>	Norway	<i>Picea abies</i>	H. Solheim; 1986	DAOM 225449	CMW 20931; CBS 100202; C 662	ex-holotype	KM495549	KM495372	KM495460
<i>C. rufipennis</i>	<i>E. rufipennis</i>	Canada	<i>Picea engelmannii</i>	H. Solheim; 1992	–	CMW 11661	original collection	KM495550	KM495373	–
<i>C. salinaria</i>	<i>H. salinaria</i>	South Africa	<i>Eucalyptus maculata</i>	G. Kamgan Nkuekam; 2007	PREM 60557	CMW 25911; CBS 129733	ex-holotype	KM495551	KM495374	KM495461
<i>C. savannae</i>	<i>H. savannae</i>	South Africa	<i>Acacia nigrescens</i>	G. Kamgan Nkuekam & J. Roux; 2005	PREM 59423	CMW 17300; CBS 121151	ex-holotype	KM495552	KM495375	KM495462
<i>C. smalleyi</i>	<i>C. smalleyi</i>	USA	<i>Carya cordiformis</i>	E. Smalley; 1993	BPI 843722	CMW 14800; CBS 114724; C 684	ex-holotype	KM495553	KM495376	KM495463
<i>C. sublaevis</i>	<i>H. sublaevis</i>	Ecuador	<i>Terminalia ivorensis</i>	M.J. Wingfield; 2004	PREM 60163	CMW 22449; CBS 122517	ex-paratype	KM495554	KM495377	KM495464
<i>C. sumatrana</i>	<i>H. sumatrana</i>	Indonesia	<i>Acacia mangium</i>	M. Tarigan; 2005	PREM 59868	CMW 21109; CBS 124011	ex-paratype	KM495555	KM495378	KM495465
<i>C. tanganyicensis</i>	<i>C. tanganyicensis</i>	Tanzania	<i>Acacia mearnsii</i>	R.N. Heath & J. Roux; 2004	–	CMW 15999; CBS 122294	ex-paratype	KM495556	KM495379	KM495466
<i>C. thulamensis</i>	<i>C. thulamensis</i>	South Africa	<i>Colophospermum mopane</i>	M. Mbenoun & J. Roux; 2010	PREM 60828	CMW 35972; CBS 131284	ex-holotype	KM495557	KM495380	KM495467
<i>C. tribiliformis</i>	<i>H. tribiliformis</i>	Indonesia	<i>Pinus merkusii</i>	M.J. Wingfield; 1996	PREM 57827	CMW 13013; CBS 115866	ex-holotype	KM495558	KM495381	KM495468
<i>C. tsitsikammensis</i>	<i>C. tsitsikammensis</i>	South Africa	<i>Rapanea melanophloeos</i>	G. Kamgan Nkuekam; 2005	PREM 59424	CMW 14276; CBS 121018	ex-holotype	KM495559	KM495382	KM495469
<i>C. tyalla</i>	<i>H. tyalla</i>	Australia	<i>Eucalyptus dunnii</i>	G. Kamgan Nkuekam & A.J. Carnegie; 2008	–	CMW 28932; CBS 128703	ex-holotype	KM495560	KM495383	KM495470
<i>C. variospora</i>	<i>C. variospora</i>	USA	<i>Quercus alba</i>	J.A. Johnson; 2001	BPI 843737	CMW 20935; CBS 114715; C 1843	ex-paratype	KM495561	KM495384	KM495471
<i>C. virescens</i>	<i>D. virescens</i>	USA	<i>Acer saccharum</i>	D. Houston; 1987	–	CMW 17339; CBS 130772; C 261	not type	KM495562	KM495385	KM495472

(continued on next page)

Table 1. (Continued)

Previous name	New name	Country	Host/substrate	Collector; collection year	Herbarium Specimen ¹	Culture collection number(s) ¹	Strain status	GenBank accession numbers ²		
								60S	LSU	MCM7
<i>C. zambeziensis</i>	<i>C. zambeziensis</i>	South Africa	<i>Acacia nigrescens</i>	M. Mbenoun & J. Roux; 2010	PREM 60826	CMW 35963; CBS 131282	ex-paratype	KM495563	KM495386	KM495473
<i>Chalaropsis</i> sp. 1	<i>Chalaropsis</i> sp. 1	Belgium	<i>Populus</i> sp.	R. Veldeman; 1975	–	CMW 22737; CBS 180.75	not type	KM495580	KM495403	KM495490
<i>Chalaropsis</i> sp. 1	<i>Chalaropsis</i> sp. 1	USA	<i>Ulmus</i> sp.	R.W. Davidson; 1939	–	CMW 22738; CBS 130.39; C 1378; MUCL 9540; RWD E-1	not type	KM495581	KM495404	KM495491
<i>Graphium fabiforme</i>	<i>Graphium fabiforme</i>	Madagascar	Dead <i>Adansonia rubrostipa</i>	J. Roux & M.J. Wingfield; 2007	PREM 60310	CMW 30626; CBS 124921	ex-holotype	KM495564	KM495387	KM495474
<i>G. fimbriisporum</i>	<i>G. fimbriisporum</i>	France	<i>Ips typographus</i> gallery, in stump of <i>Picea abies</i>	M. Morelet; 1992	PFN 1494	CMW 5605; CBS 870.95; MPFN 281-8	ex-holotype	KM495565	KM495388	KM495475
<i>G. laricis</i>	<i>G. laricis</i>	Austria	Synnemata occurring in galleries of the bark beetle <i>Ips cembrae</i>	T. Kirisits & P. Baier; 1995	DAOM 229757	CMW 5601; CBS 116194; DAOM 229757; IFFF ICL/MEA/13	ex-holotype	KM495566	KM495389	KM495476
<i>G. pseudormiticum</i>	<i>G. pseudormiticum</i>	South Africa	<i>Pinus</i> sp.	M.J. Wingfield; 1984	PREM 51539	CMW 503	ex-holotype	KM495567	KM495390	KM495477
<i>Huntiella chlamydoformis</i> nom. prov.	<i>H. chlamydoformis</i> nom. prov.	Cameroon	<i>Theobromae cacao</i>	M. Mbenoun & J. Roux; 2009	PREM 60837	CMW 36932; CBS 131674	ex-holotype	KM495505	KM495328	KM495417
<i>H. pycnanthi</i> nom. prov.	<i>H. pycnanthi</i> nom. prov.	Cameroon	<i>Theobromae cacao</i>	M. Mbenoun; 2009	PREM 60835	CMW 36916; CBS 131672	ex-holotype	KM495547	KM495370	KM495458
<i>Knoxdaviesia capensis</i>	<i>Knoxdaviesia capensis</i>	South Africa	<i>Protea longifolia</i>	M.J. Wingfield; 1984	–	CMW 997; CBS 120015	not type	KM495568	KM495391	KM495478
<i>K. cecropiae</i>	<i>K. cecropiae</i>	Costa Rica	<i>Cecropia angustifolia</i>	L. Kirkendall & J. Hulcr; 2005	PRM 858080	CMW 22991; CCF 3565	ex-holotype	KM495569	KM495392	KM495479
<i>K. proteae</i>	<i>K. proteae</i>	South Africa	<i>Protea repens</i> flower infested with insects	L.J. Strauss; 1985	PREM 48924	CMW 738; CBS 486.88	ex-holotype	KM495570	KM495393	KM495480
<i>K. serotectus</i>	<i>K. serotectus</i>	South Africa	Grow on insect (<i>Cossonus</i> sp.) found in <i>Euphorbia ingens</i>	J.A. van der Linde & J. Roux; 2009	PREM 60566	CMW 36767; CBS 129738	ex-holotype	KM495571	KM495394	KM495481
<i>K. ubusi</i>	<i>K. ubusi</i>	South Africa	Insect tunnels in <i>Euphorbia tetragona</i>	J. Roux; 2010	PREM 60568	CMW 36769; CBS 129742	ex-holotype	KM495572	KM495395	KM495482
<i>Thielaviopsis australis</i>	<i>D. australis</i>	Australia	<i>Nothofagus cunninghamii</i>	M. Hall; 2001	–	CMW 2333	not type	KM495573	KM495396	KM495483
<i>T. basicola</i>	<i>T. basicola</i>	Netherlands	<i>Lathyrus odoratus</i>	G.A. van Arkel; –	–	CMW 7068; CBS 413.52	not type	KM495574	KM495397	KM495484
<i>T. ceramica</i>	<i>H. ceramica</i>	Malawi	<i>Eucalyptus grandis</i>	R.N. Heath & J. Roux; 2004	PREM 59808	CMW 15245; CBS 122299; CMW 15251	ex-holotype	KM495575	KM495398	KM495485
<i>T. euricoi</i>	<i>T. euricoi</i>	Brazil	Air	E.A.F. da Matta; 1956	URM 640	CMW 28537; CBS 893.70; MUCL 1887; UAMH 1382	ex-holotype	KM495517	KM495340	KM495429
<i>T. neocaledoniae</i>	<i>D. neocaledoniae</i>	New Caledonia	<i>Coffea robusta</i>	R. Dadant; 1948	–	CMW 3270; CBS 149.83; C 694	ex-holotype	KM495576	KM495399	KM495486

(continued on next page)

Table 1. (Continued)

Previous name	New name	Country	Host/substrate	Collector; collection year	Herbarium Specimen ¹	Culture collection number(s) ¹	Strain status	GenBank accession numbers ²		
								60S	LSU	MCM7
<i>T. ovoidea</i>	<i>Chalaropsis ovoidea</i>	Netherlands	Firewood	W. Gams; 1976	–	CMW 22733; CBS 354.76; C 1375	not type	KM495577	KM495400	KM495487
<i>T. ovoidea</i>	<i>Ch. ovoidea</i>	Germany	<i>Quercus petraea</i>	H. Kleinhempel; 1987	–	CMW 22732; CBS 136.88	not type	KM495578	KM495401	KM495488
<i>T. Thielavioides</i>	<i>Ch. thielavioides</i>	Italy	<i>Lupinus albus</i>	R. Ciferri; 1937	–	CMW 22736; CBS 148.37; MUCL 6235	not type	KM495579	KM495402	KM495489

¹ ATCC: American Type Culture Collection, Virginia, U.S.A.; BPI: US National Fungus Collections, Systematic Botany and Mycology Laboratory, Maryland, U.S.A.; C: Culture collection of T.C. Harrington, Iowa State University, U.S.A.; CBS: Culture collection of the CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CCF: Culture Collection of Fungi, Department of Botany, Faculty of Science, Charles University, Prague, Czech Republic; CMW: Culture collection Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa; DAOM: Plant Research Institute, Department of Agriculture (Mycology), Ottawa, Canada; DAR: New South Wales, Plant Pathology Herbarium, Australia; DLS: Culture collection of D. Six, University of Montana, U.S.A.; FP: Rocky Mountain Forest & Range Experimental Station Herbarium, Fort Collins, Colorado, U.S.A.; IFFF: Culture collection of the Institute of Forest Entomology, Forest Pathology and Forest Protection (IFFP), University of Natural Resources and Applied Life Sciences, Vienna (BOKU), Vienna, Austria; IMI: International Mycological Institute, CAB International, Wellesbourne, Warwick, United Kingdom; JCM: Japan Collection of Micro-organisms, RIKEN BioResource Center, Japan; MAFF: Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Ibaraki, Japan; MPFN: Culture collection at the Laboratoire de Pathologie Forestière, INRA, Centre de Recherches de Nancy, 54280 Champenoux, France; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium; NIAES: National Institute for Agro-Environmental Sciences, 3-1-3 Kannondai, Tsukuba, 305-8604, Japan; PREM: National Collection of Fungi, Pretoria, South Africa; PRM: Corda Herbarium, Prague, Czech Republic; Redfern: Culture Collection of D.B. Redfern, Forestry Commission, Northern Research Station, Roslin, Midlothian, UK; RWD: Culture collection of R.W. Davidson, Department of Forest and Wood Sciences, Colorado State University, Fort Collins, Colorado; UAMH: University of Alberta Microfungus Collection and Herbarium, Edmonton, Alberta, Canada; URM: Father Camille Torrend Herbarium-URM (previously University of Recife Herbarium), Department of Mycology, Universidade Federal de Pernambuco, Recife, Brazil.

² 60S: partial 60S ribosomal protein RPL10 gene; LSU: partial nuclear ribosomal DNA large subunit (28S); MCM7: partial mini-chromosome maintenance complex component 7 gene.

temperatures (between 52 °C and 60 °C) until successful amplification was obtained. Direct sequencing of PCR products was done using BigDye[®] Terminator v. 3.1 Cycle Sequencing kit (Applied Biosystems) with a 1/16 reaction and at 55 °C annealing temperature for all primers. Sequencing PCR products were precipitated using the sodium acetate and ethanol precipitation protocol, followed by fragment separation using an ABI PRISM[®] 3100 Genetic Analyzer (Applied Biosystems).

Phylogenetic analyses

Sequences from different gene regions were aligned using an online version of MAFFT v. 7 (Katoch & Standley 2013). The three gene regions (LSU, 60S and MCM7) were combined and analysed as a single dataset. Each of the gene regions was also analysed separately and results were compared with those of the combined analyses. Maximum parsimony (MP) analyses were performed in MEGA6 (Tamura *et al.* 2013) with 1000 bootstrap replications. The subtree-pruning-regrafting (SPR) algorithm was selected, and alignment gaps and missing data included. Maximum likelihood (ML) analyses were done using raxmlGUI (Silvestro & Michalak 2012) with the GTR+G+I substitution model selected. Ten parallel runs with four threads and 1000 bootstrap replications were conducted. Bayesian inference (BI) analyses were performed using MrBayes v. 3.2 (Ronquist *et al.* 2012) employing the GTR+G+I substitution model. Ten parallel runs, each with four chains, were conducted. Trees were sampled at every 100th generation for 5 M generations. After sampling, 25 % of trees were discarded as a burn-in phase and posterior probabilities were calculated from all the remaining trees.

Morphology

Morphological descriptions from the protologues of all species treated in this study were carefully considered when genera were redefined. Based on these species descriptions, the most common characters of all species in a genus were selected and incorporated in the emended and new genus descriptions. Over time, different authors often used different terminology describing similar characters. We aligned the generic descriptions of the different genera with each other using similar terminology.

RESULTS

Maximum likelihood, BI and MP trees obtained from analyses of the individual gene regions (Figs 4–6) and the combined datasets (Fig. 7) of the LSU, 60S and MCM7 sequences, consistently resulted in nine well-supported major lineages. Although trees derived from individual datasets had different topologies (Figs 4–6), they were not significantly incongruent with the trees obtained from the combined analyses (Fig. 7). This was indicated by the fact that most major lineages found in the combined analyses were present in trees resulting from individual datasets. Only few exceptions were observed in the cases of 60S and LSU datasets. In one exceptional case, the 60S dataset (Fig. 5) showed Lineage 6 as split into two clades. In another case, the LSU tree (Fig. 4) depicted lineage 5 as not being monophyletic, although isolates belonging to this lineage still grouped relatively

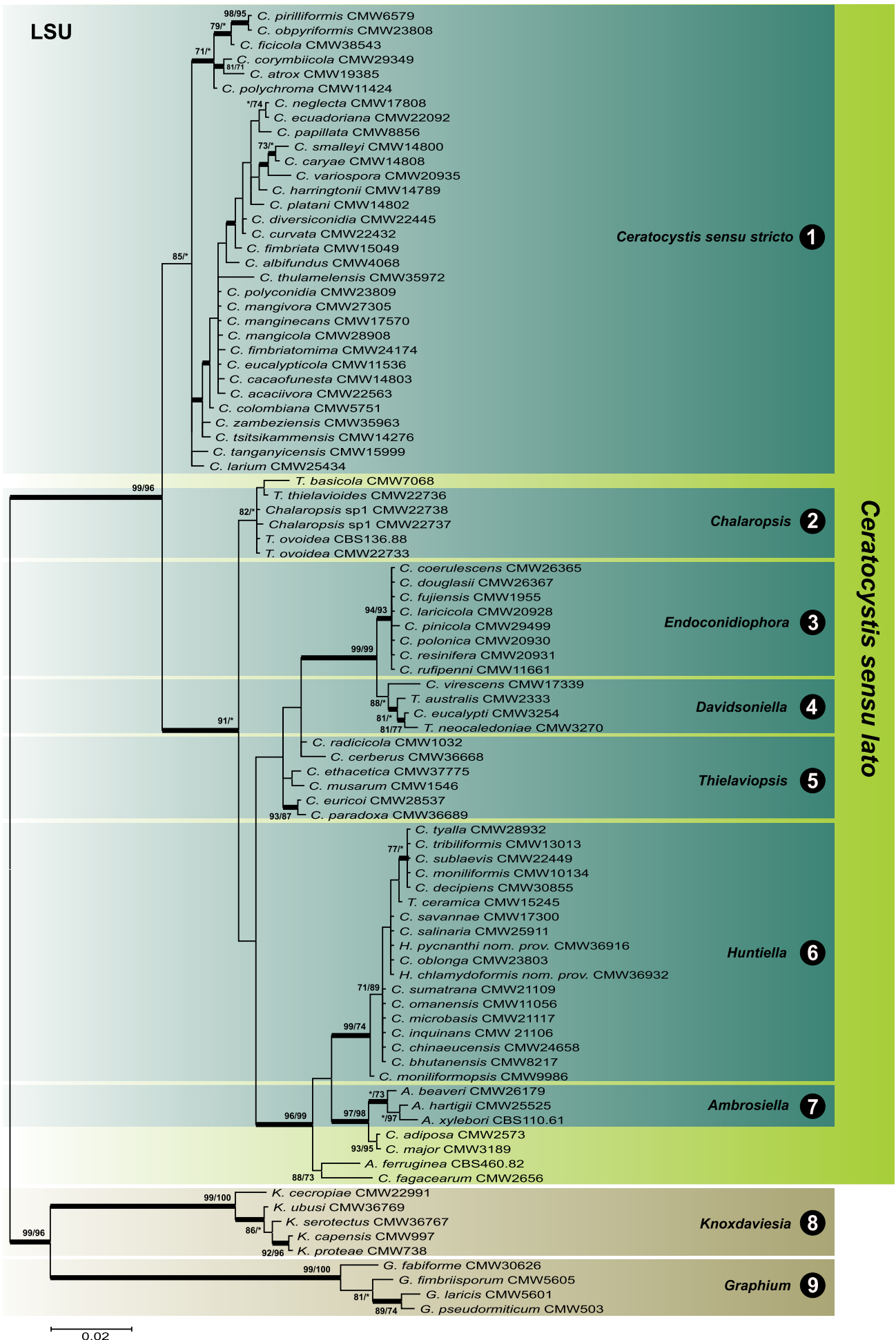


Fig. 4. Bayesian phylogram derived from analyses of the aligned LSU dataset containing 898 characters, of which 164 were parsimony informative. Thick branches represent BI posterior probabilities $\geq 95\%$. Bootstrap support values $\geq 70\%$ are indicated at nodes as MP/ML. * = no bootstrap support or bootstrap support values $< 70\%$.

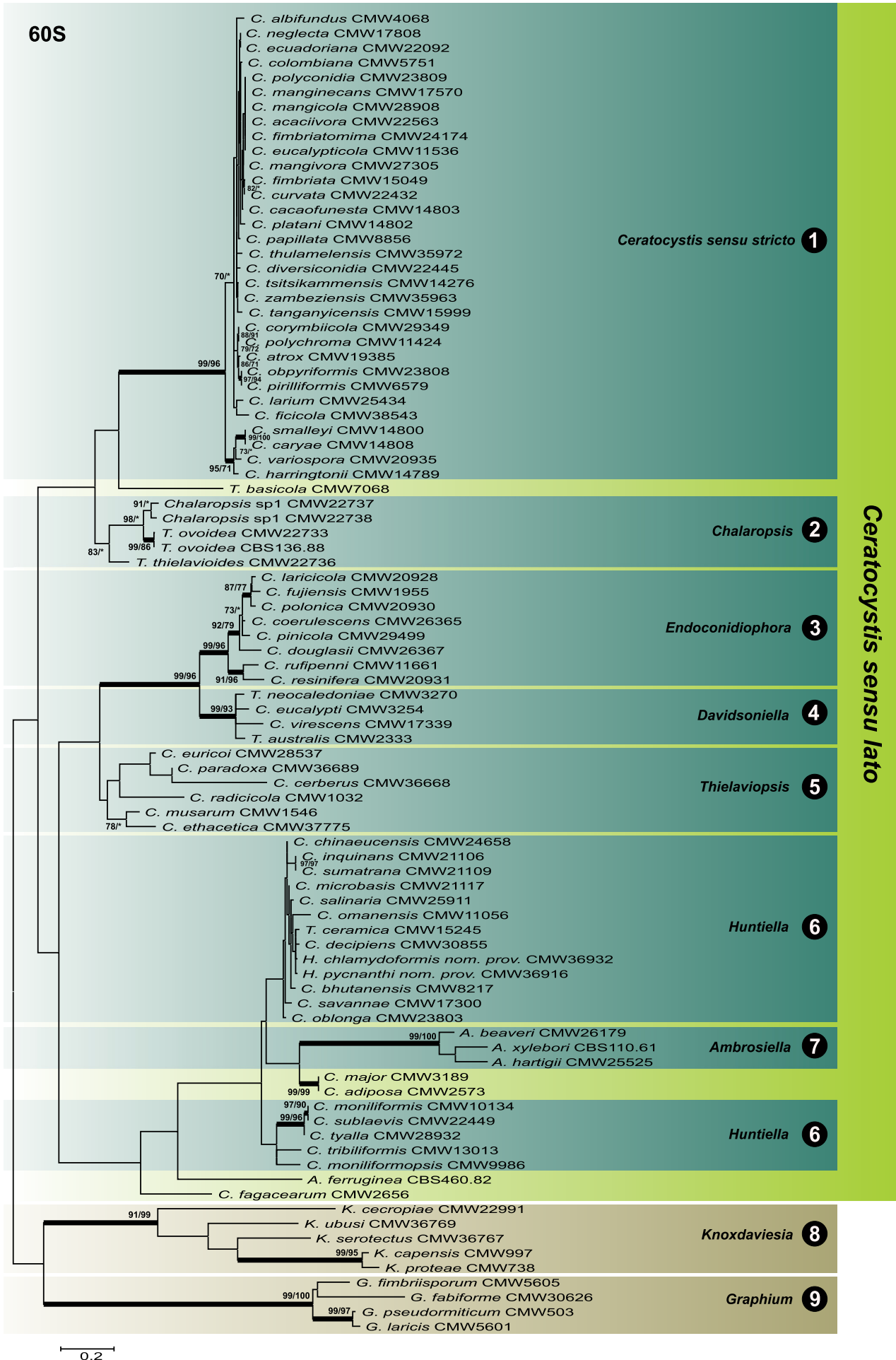


Fig. 5. RAxML phylogram derived from analyses of the aligned 60S dataset containing 711 characters, of which 258 were parsimony informative. Thick branches represent BI posterior probabilities $\geq 95\%$. Bootstrap support values $\geq 70\%$ are indicated at nodes as MP/ML. * = no bootstrap support or bootstrap support values $< 70\%$.

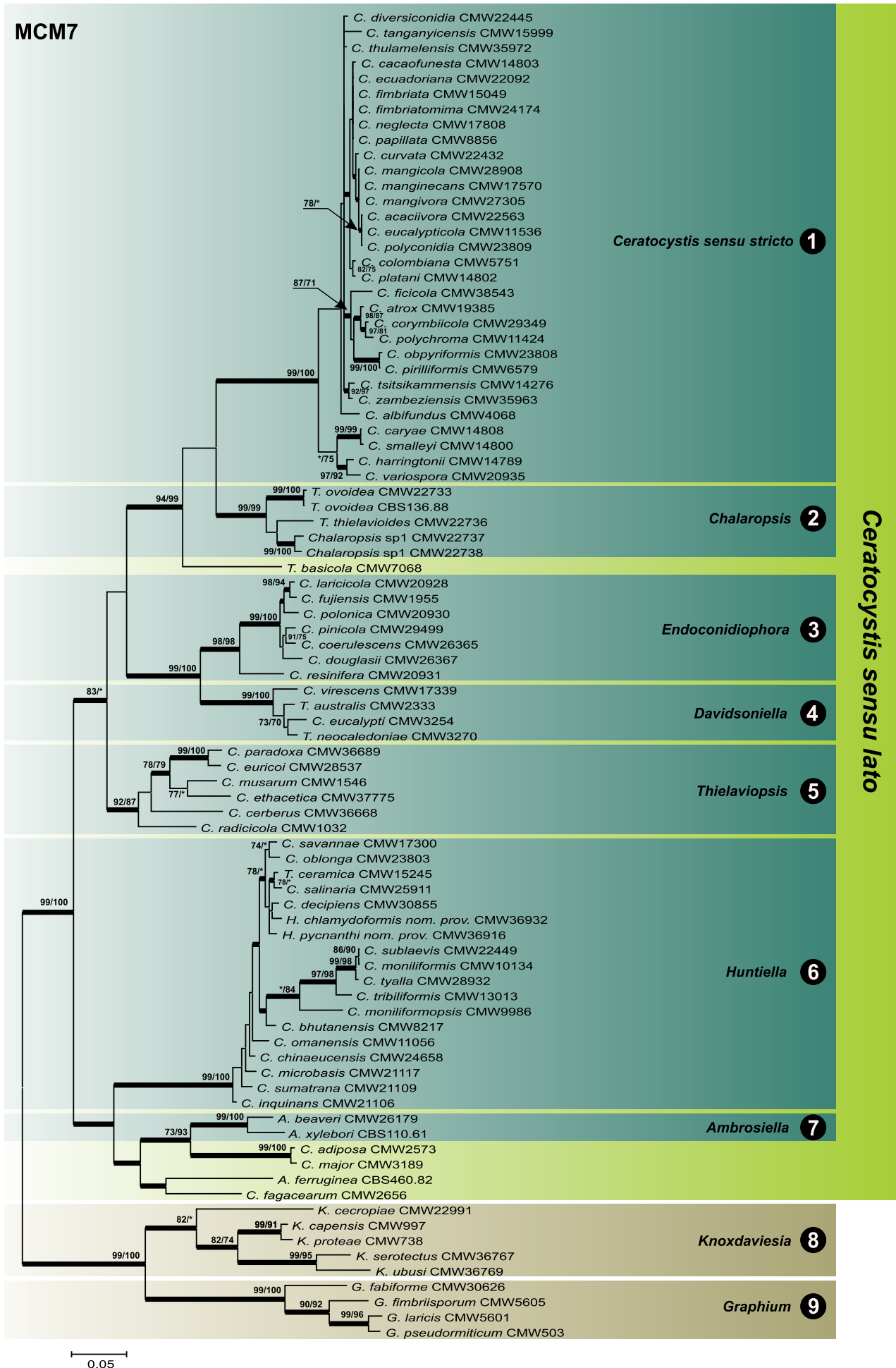


Fig. 6. Bayesian phylogram derived from analyses of MCM7 dataset containing 628 characters, of which 313 were parsimony informative. Thick branches represent BI posterior probabilities $\geq 95\%$. Bootstrap support values $\geq 70\%$ are indicated at nodes as MP/ML. * = no bootstrap support or bootstrap support values $< 70\%$.

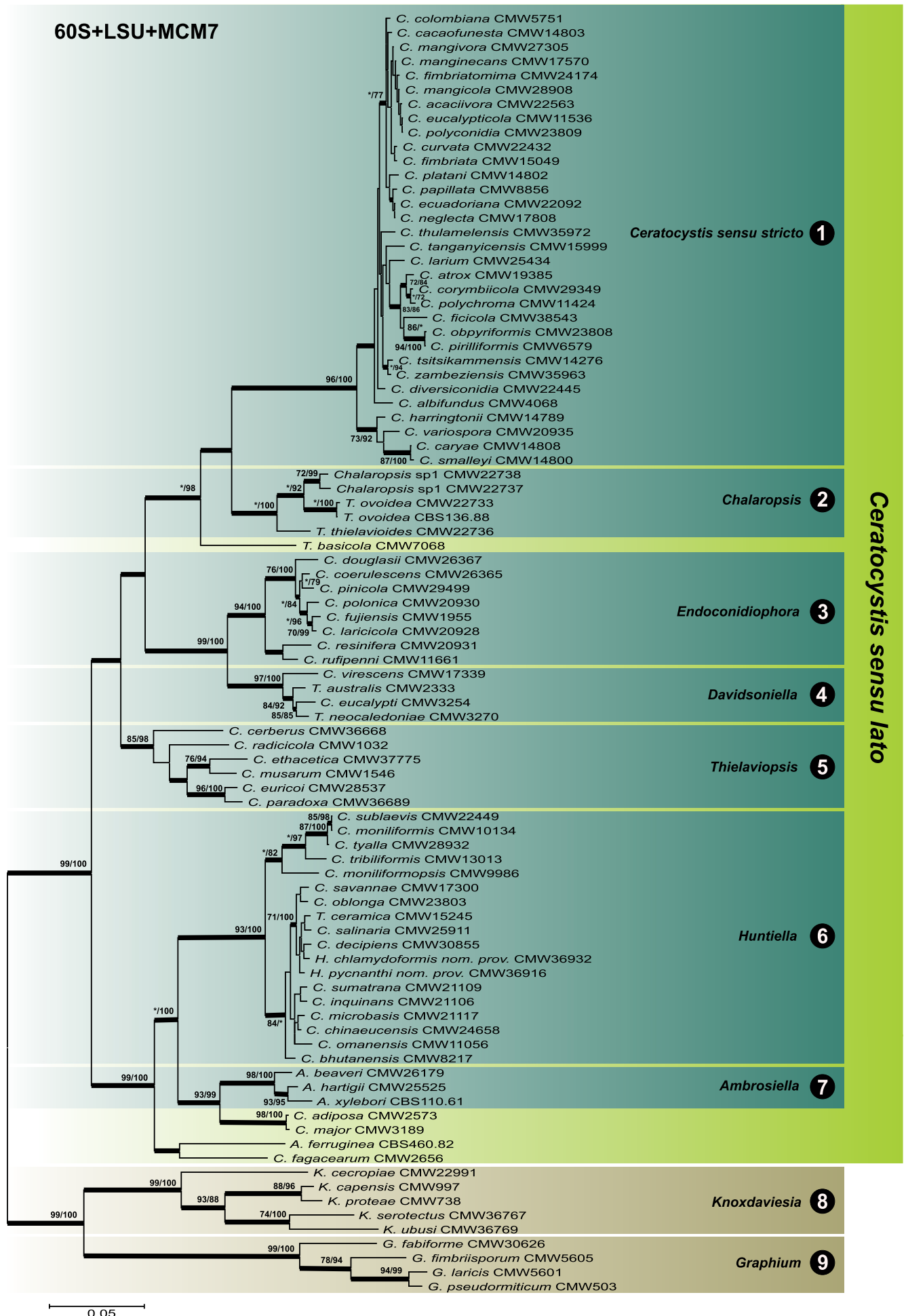


Fig. 7. Bayesian phylogram derived from analyses of the concatenated dataset (60S, LSU and MCM7) containing 2 237 characters, of which 735 were parsimony informative. Thick branches represent BI posterior probabilities $\geq 95\%$. Bootstrap support values $\geq 70\%$ are indicated at nodes as MP/ML. * = no bootstrap support or bootstrap support values $< 70\%$.

close to each other. Neither of these placements, however, was supported by phylogenetic statistics. Among the three gene regions used, MCM7 proved to be the most informative and resulted in trees with topologies similar to those obtained from the combined dataset.

The first of the nine lineages (Figs 4–7), representing the largest number of species, included *C. fimbriata* (type species of *Ceratocystis*) and 31 other species previously included in the *C. fimbriata* complex. The second lineage included CMW 22736, representing *T. thielavioides* (type species for *Chalaropsis*), *T. ovoidea*, and two isolates from the USA and Belgium, previously described as *T. thielavioides*, but clearly distinct from CMW 22736. These two isolates are thus referred to as *Chalaropsis* sp. 1. The third lineage included *C. coerulescens*, type species for *Endoconidiophora*, and seven species previously considered part of the *C. coerulescens* complex. Isolates representing *C. virescens*, *C. eucalypti*, *T. australis* and *T. neocaledoniae* represented the fourth lineage, which did not include a type species of a previously described genus. Lineage 5 was previously referred to as the *C. paradoxa* complex, and included *C. ethacetica* (type species of *Thielaviopsis*), *C. euricoi*, *C. musarum*, *C. radicola* and the recently described species, *C. cerberus*. The sixth lineage was the second largest and included *C. moniliformis* s. str. and 17 other species, but contained no type species representing a previously described genus. Two new species that are currently being described (Mbenoun *et al.*, unpubl. data) grouped in this lineage, and were labelled according to provisional species names provided by M. Mbenoun (unpublished), namely *Huntiella chlamydospora* nom. prov. and *H. pycnanthi* nom. prov. Isolates of *Ambrosiella xylebori* (type species for *Ambrosiella*), *A. hartigii* and *A. beaveri* formed a distinct lineage. The last two lineages comprised *Knoxdaviesia* and *Graphium* species used as outgroups in all analyses.

Five of the 79 species in *Ceratocystis* s. l. were not accommodated in any of the nine major lineages discussed above (Figs 4–7). *Ceratocystis adiposa* and *C. major* had identical sequences in ITS (data not shown), LSU and 60S, and formed a distinct clade that was most closely related to lineage 7 (representing *Ambrosiella*). *Ceratocystis fagacearum* and *A. ferruginea*, although significantly different from each other, formed a clade of their own separating them from other *Ceratocystis* and *Ambrosiella* lineages. The fifth species, *T. basicola*, formed a unique lineage distinct from, but related to species in lineage 2 as its closest relatives.

GENERIC DESCRIPTIONS AND NOMENCLATOR

Phylogenetic data generated in this study revealed seven well-supported lineages in *Ceratocystis* s. l. The distinction between these lineages is also supported by morphological and ecological data for the species in these groups. These lineages are, therefore, treated as distinct genera. Five of the lineages incorporate the type species of earlier described genera, and we thus emend the descriptions of *Ambrosiella*, *Ceratocystis* s. str., *Chalaropsis*, *Endoconidiophora*, and *Thielaviopsis*, based on the types and other species accommodated in the lineages. Two lineages for which existing names are not available are treated as novel genera, described here as *Davidsoniella* and *Huntiella*. Where necessary, new combinations are provided for the names

of species in these genera. Species previously treated in *Ceratocystis*, but excluded from the newly defined genera in the *Ceratocystidaceae* (Tables 2 and 3), invalidly described species (Table 4), and homonyms from kingdoms other than the Fungi (Table 5), are not treated in the nomenclator, but listed in the tables as indicated.

Ambrosiella Brader ex Arx & Hennebert, Mycopath. Mycol. Appl. 25: 314. 1965.

?= *Phialophoropsis* L.R. Batra, Mycologia 59: 1008. 1967. (type species *Ph. trypodendri*).

Type species: Ambrosiella xylebori Brader ex Arx & Hennebert, Mycopath. Mycol. Appl. 25: 314. 1965.

Sexual state not known. *Conidiophores* phialidic, single to aggregated in sporodochia, hyaline, unbranched or sparingly branched, one-celled to septate. *Conidia* formed in chains or as terminal aleurioconidia.

Notes: We followed the emended generic description for *Ambrosiella* by Harrington *et al.* (2010), who restricted the genus to those species belonging to the *Microascales*. DNA sequence data is not available for *A. trypodendri*, type species of *Phialophoropsis*, which means the synonymy of the latter genus with *Ambrosiella* cannot be confirmed for the present. All known *Ambrosiella* species are associates of ambrosia beetles.

Ambrosiella beaveri Six, Z.W. de Beer & W.D. Stone, Antonie van Leeuwenhoek 96: 23. 2009.

Note: Sexual state unknown.

Ambrosiella hartigii L.R. Batra, Mycologia 59: 998. 1967.

Note: Sexual state unknown.

Ambrosiella roeperii T.C. Harr. & McNew, Mycologia 106: 841. 2014.

Notes: Sexual state unknown. Sequences of this newly described species were not included in our analyses, but Harrington *et al.* (2014b) clearly showed that this species groups within *Ambrosiella*.

Ambrosiella trypodendri (L.R. Batra) T.C. Harr., Mycotaxon 111: 355. 2010

Basionym: Phialophoropsis trypodendri L.R. Batra, Mycologia 59: 1008. 1967.

Notes: Sexual state unknown. *Ambrosiella trypodendri* is the type species of *Phialophoropsis* (Batra 1967). No cultures are available for this species. However, Harrington *et al.* (2010) argued that it is morphologically similar to *Ambrosiella* and provided a new combination for it. Seifert has examined the type, and made a drawing from it that was used to represent this species in *The Genera of Hyphomycetes* (Seifert *et al.* 2011).

Ambrosiella xylebori Brader ex Arx & Hennebert, Mycopath. Mycol. Appl. 25: 314. 1965.

Table 2. Species previously treated in *Ceratocystis*, but now excluded from the genus because they were shown to belong to other genera. More details on each species are presented by [De Beer et al. \(2013b\)](#).

Name in <i>Ceratocystis</i>	Current name	Basionym
<i>C. abiocarpa</i> R.W. Davidson	<i>Grosmannia abiocarpa</i> (R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis abiocarpa</i> R.W. Davidson
<i>C. adjuncti</i> R.W. Davidson	<i>Ophiostoma adjuncti</i> (R.W. Davidson) Harrington	<i>Ceratocystis adjuncti</i> R.W. Davidson
<i>C. albida</i> (Math.-Käärik) J. Hunt	synonym of <i>Ophiostoma stenoceras</i> (Robak) Nannf.	<i>Ophiostoma albidum</i> Math.-Käärik
<i>C. allantospora</i> H.D. Griffin	<i>Ophiostoma allantosporum</i> (Griffin) M. Villarreal	<i>Ceratocystis allantospora</i> H.D. Griffin
<i>C. ambrosia</i> Bakshi	<i>Ophiostoma ambrosium</i> (Bakshi) Hausner, J. Reid & Klassen	<i>Ceratocystis ambrosia</i> Bakshi
<i>C. angusticollis</i> Wright & H.D. Griffin	<i>Ophiostoma angusticollis</i> (Wright & Griffin) M. Villarreal	<i>Ceratocystis angusticollis</i> Wright & H.D. Griffin
<i>C. araucariae</i> Butin	<i>Ophiostoma araucariae</i> (Butin) de Hoog & Scheffer	<i>Ceratocystis araucariae</i> Butin
<i>C. arborea</i> Olchow. & J. Reid	<i>Ophiostoma arborea</i> (Olchow. & J. Reid) Yamaoka & M.J. Wingf.	<i>Ceratocystis arborea</i> Olchow. & J. Reid
<i>C. aurea</i> (R.C. Rob. & R.W. Davidson) H.P. Upadhyay	<i>Grosmannia aurea</i> (R.C. Rob. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Europhium aureum</i> R.C. Rob. & R.W. Davidson
<i>C. bacillospora</i> Butin & G. Zimm.	<i>Ophiostoma bacillosporum</i> (Butin & G. Zimm.) de Hoog & Scheffer	<i>Ceratocystis bacillospora</i> Butin & G. Zimm.
<i>C. bicolor</i> (R.W. Davidson & Wells) R.W. Davidson	<i>Ophiostoma bicolor</i> R.W. Davidson & D.E. Wells	<i>Ophiostoma bicolor</i> R.W. Davidson & D.E. Wells
<i>C. brunnea</i> R.W. Davidson	<i>Ophiostoma brunneum</i> (R.W. Davidson) Hausner & J. Reid	<i>Ceratocystis brunnea</i> R.W. Davidson
<i>C. brunneo-ciliata</i> (Math.-Käärik) J. Hunt	<i>Ophiostoma brunneo-ciliatum</i> Math.-Käärik	<i>Ophiostoma brunneo-ciliatum</i> Math.-Käärik
<i>C. brunneocrinita</i> E.F. Wright & Cain	<i>Graphilbum brunneocrinitum</i> (E.F. Wright & Cain) Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis brunneocrinita</i> E.F. Wright & Cain
<i>C. cainii</i> Olchow. & J. Reid	<i>Grosmannia cainii</i> (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis cainii</i> Olchow. & J. Reid
<i>C. californica</i> DeVay, R.W. Davidson & Moller	<i>Ophiostoma californicum</i> (DeVay, R.W. Davidson & Moller) Hausner, J. Reid & Klassen	<i>Ceratocystis californica</i> DeVay, R.W. Davidson & Moller
<i>C. cana</i> (Münch) Moreau	<i>Ophiostoma canum</i> (Münch) Syd.	<i>Ceratostomella cana</i> Münch
<i>C. capitata</i> H.D. Griffin	synonym of <i>Ophiostoma tenellum</i> (R.W. Davidson) M. Villarreal	<i>Ceratocystis capitata</i> H.D. Griffin
<i>C. castaneae</i> (Vanin & Solovjev) C. Moreau	<i>Ophiostoma castaneae</i> (Vanin & Solovjev) Nannf.	<i>Ceratostomella castaneae</i> Vanin & Solovjev
<i>C. catoniana</i> (Goid.) C. Moreau	<i>Ophiostoma catonianum</i> (Goid.) Goid.	<i>Ceratostomella catoniana</i> Goid.
<i>C. clavata</i> (Math.) Hunt	<i>Ophiostoma clavatum</i> Math.	<i>Ophiostoma clavatum</i> Math.
<i>C. clavigera</i> (R.C. Rob. & R.W. Davidson) H.P. Upadhyay	<i>Grosmannia clavigera</i> (R.C. Rob. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Europhium clavigerum</i> R.C. Rob. & R.W. Davidson
<i>C. columnaris</i> Olchow. & J. Reid	<i>Ophiostoma columnare</i> (Olchow. & J. Reid) Seifert & G. Okada	<i>Ceratocystis columnaris</i> Olchow. & J. Reid
<i>C. concentrica</i> Olchow. & J. Reid	<i>Ceratocystiopsis concentrica</i> (Olchow. & J. Reid) H.P. Upadhyay	<i>Ceratocystis concentrica</i> Olchow. & J. Reid
<i>C. conicollis</i> Olchow. & J. Reid	<i>Ceratocystiopsis conicollis</i> (Olchow. & J. Reid) H.P. Upadhyay	<i>Ceratocystis conicollis</i> Olchow. & J. Reid
<i>C. coronata</i> Olchow. & J. Reid	<i>Ophiostoma coronatum</i> (Olchow. & J. Reid) M. Villarreal	<i>Ceratocystis coronata</i> Olchow. & J. Reid
<i>C. crassivaginata</i> H.D. Griffin	<i>Grosmannia crassivaginata</i> (H.D. Griffin) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis crassivaginata</i> H.D. Griffin
<i>C. crenulata</i> Olchow. & J. Reid	<i>Ophiostoma crenulatum</i> (Olchow. & J. Reid) Hausner & J. Reid	<i>Ceratocystis crenulata</i> Olchow. & J. Reid
<i>C. curvicollis</i> Olchow. & J. Reid	<i>Graphilbum curvicolle</i> (Olchow. & J. Reid) Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis curvicollis</i> Olchow. & J. Reid
<i>C. davidsonii</i> Olchow. & J. Reid	<i>Grosmannia davidsonii</i> (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis davidsonii</i> Olchow. & J. Reid
<i>C. denticulata</i> R.W. Davidson	<i>Ophiostoma denticulatum</i> (R.W. Davidson) Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis denticulata</i> R.W. Davidson
<i>C. distorta</i> R.W. Davidson	<i>Ophiostoma distortum</i> (R.W. Davidson) de Hoog & Scheffer	<i>Ceratocystis distorta</i> R.W. Davidson

(continued on next page)

Table 2. (Continued).

Name in <i>Ceratocystis</i>	Current name	Basionym
<i>C. dolominuta</i> H.D. Griffin	synonym of <i>Ceratocystiopsis minuta</i> (Siemaszko) H.P. Upadhyay & W.B. Kendr.	<i>Ceratocystis dolominuta</i> H.D. Griffin
<i>C. dryocoetidis</i> W.B. Kendr. & Molnar	<i>Grosmannia dryocoetidis</i> (W.B. Kendr. & Molnar) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis dryocoetidis</i> W.B. Kendr. & Molnar
<i>C. epigloea</i> Guerrero	<i>Ophiostoma epigloeum</i> (Guerrero) de Hoog	<i>Ceratocystis epigloea</i> Guerrero
<i>C. eucastaneae</i> R.W. Davidson	synonym of <i>Ophiostoma stenoceras</i> (Robak) Nannf.	<i>Ceratocystis eucastaneae</i> R.W. Davidson
<i>C. europhioides</i> E.F. Wright & Cain	<i>Grosmannia europhioides</i> (E.F. Wright & Cain) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis europhioides</i> E.F. Wright & Cain
<i>C. fagi</i> (W. Loos) C. Moreau	synonym of <i>Ophiostoma quercus</i> (Georgev.) Nannf.	<i>Ceratostomella fagi</i> W. Loos
<i>C. falcata</i> E.F. Wright & Cain	<i>Cornuvesica falcata</i> (E.F. Wright & Cain) C.D. Viljoen, M.J. Wingf. & K. Jacobs	<i>Ceratocystis falcata</i> E.F. Wright & Cain
<i>C. fasciata</i> Olchow. & J. Reid	<i>Ophiostoma fasciatum</i> (Olchow. & J. Reid) Hausner, J. Reid & Klassen	<i>Ceratocystis fasciata</i> Olchow. & J. Reid
<i>C. fimicola</i> (Marchal) H.P. Upadhyay	<i>Sphaeronaemella fimicola</i> Marchal	<i>Sphaeronaemella fimicola</i> Marchal
<i>C. floccosa</i> (Math.) J. Hunt	<i>Ophiostoma floccosum</i> Math.	<i>Ophiostoma floccosum</i> Math.
<i>C. francke-grosmanniae</i> R.W. Davidson	<i>Grosmannia francke-grosmanniae</i> (R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis francke-grosmanniae</i> R.W. Davidson
<i>C. fraxinopennsylvanica</i> T.E. Hinds	<i>Togninia fraxinopennsylvanica</i> (T.E. Hinds) Hausner, Eyjólfssdóttir & J. Reid	<i>Ceratocystis fraxinopennsylvanica</i> T.E. Hinds
<i>C. galeiformis</i> Bakshi	<i>Grosmannia galeiformis</i> (B.K. Bakshi) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis galeiformis</i> Bakshi
<i>C. gossypina</i> R.W. Davidson	<i>Ophiostoma gossypinum</i> (R.W. Davidson) J. Taylor	<i>Ceratocystis gossypina</i> R.W. Davidson
<i>C. gossypina</i> var. <i>robusta</i> R.W. Davidson	synonym of <i>Ophiostoma stenoceras</i> (Robak) Nannf.	<i>Ceratocystis gossypina</i> var. <i>robusta</i> R.W. Davidson
<i>C. grandifoliae</i> R.W. Davidson	<i>Grosmannia grandifoliae</i> (R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis grandifoliae</i> R.W. Davidson
<i>C. helvellae</i> (P. Karst.) H.P. Upadhyay	<i>Sphaeronaemella helvellae</i> (P. Karst.) P. Karst.	<i>Sphaeria helvellae</i> P. Karst.
<i>C. horanszkyi</i> Tóth	<i>Sphaeronaemella horanszkyi</i> (Tóth) Tóth	<i>Ceratocystis horanszkyi</i> Tóth
<i>C. huntii</i> R.C. Rob.	<i>Grosmannia huntii</i> (R.C. Rob.) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis huntii</i> R.C. Rob.
<i>C. hyalothecium</i> R.W. Davidson	<i>Ophiostoma hyalothecium</i> (R.W. Davidson) Hausner, J. Reid & Klassen	<i>Ceratocystis hyalothecium</i> R.W. Davidson
<i>C. introcitrina</i> Olchow. & J. Reid	<i>Ophiostoma introcitrinum</i> (Olchow. & J. Reid) Hausner, J. Reid & Klassen	<i>Ceratocystis introcitrina</i> Olchow. & J. Reid
<i>C. ips</i> (Rumbold) C. Moreau	<i>Ophiostoma ips</i> (Rumbold) Nannf.	<i>Ceratostomella ips</i> Rumbold
<i>C. leptographioides</i> (R.W. Davidson) J. Hunt	<i>Grosmannia leptographioides</i> (R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratostomella leptographioides</i> R.W. Davidson
<i>C. leucocarpa</i> R.W. Davidson	<i>Ophiostoma leucocarpum</i> (R.W. Davidson) Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis leucocarpa</i> R.W. Davidson
<i>C. longirostellata</i> Bakshi	<i>Ophiostoma longirostellatum</i> (Bakshi) Arx & E. Müll.	<i>Ceratocystis longirostellata</i> Bakshi
<i>C. longispora</i> Olchow. & J. Reid	<i>Ceratocystiopsis longispora</i> (Olchow. & J. Reid) H.P. Upadhyay	<i>Ceratocystis longispora</i> Olchow. & J. Reid
<i>C. macrospora</i> Aoshima [<i>nom. inval.</i> , Art. 29.1, 36.1]	synonym of <i>Grosmannia laricis</i> (K. van der Westh., Yamaoka & M.J. Wingf.) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis macrospora</i> Aoshima [<i>nom. inval.</i> , Art. 29.1, 36.1]
<i>C. megalobrunnea</i> R.W. Davidson & Toole	<i>Ophiostoma megalobrunneum</i> (R.W. Davidson & Toole) de Hoog & Scheffer	<i>Ceratocystis megalobrunnea</i> R.W. Davidson & Toole
<i>C. microspora</i> (Arx) R.W. Davidson	<i>Ophiostoma microsporum</i> Arx	<i>Ophiostoma microsporum</i> Arx
<i>C. minima</i> Olchow. & J. Reid	<i>Ceratocystiopsis minima</i> (Olchow. & J. Reid) H.P. Upadhyay	<i>Ceratocystis minima</i> Olchow. & J. Reid
<i>C. minor</i> (Hedgc.) J. Hunt	<i>Ophiostoma minus</i> (Hedgc.) Syd.	<i>Ceratostomella minor</i> Hedgc.
<i>C. minuta</i> (Siemaszko) J. Hunt	<i>Ceratocystiopsis minuta</i> (Siemaszko) H.P. Upadhyay & W.B. Kendr.	<i>Ophiostoma minutum</i> Siemaszko
<i>C. minuta-bicolor</i> R.W. Davidson	<i>Ceratocystiopsis minuta-bicolor</i> (R.W. Davidson) H.P. Upadhyay & W.B. Kendr.	<i>Ceratocystis minuta-bicolor</i> R.W. Davidson
<i>C. montia</i> (Rumbold) J. Hunt	<i>Ophiostoma montium</i> (Rumbold) Arx	<i>Ceratostomella montium</i> Rumbold

(continued on next page)

Table 2. (Continued).

Name in <i>Ceratocystis</i>	Current name	Basionym
<i>C. multiannulata</i> (Hedgc. & R.W. Davidson) J. Hunt	<i>Ophiostoma multiannulatum</i> (Hedgc. & R.W. Davidson) Hendrix	<i>Ceratostomella multiannulata</i> Hedgc. & R.W. Davidson
<i>C. narcissi</i> (Limber) J. Hunt	<i>Ophiostoma narcissi</i> Limber	<i>Ophiostoma narcissi</i> Limber
<i>C. nigra</i> R.W. Davidson	<i>Graphilbum nigrum</i> (R.W. Davidson), Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis nigra</i> R.W. Davidson
<i>C. nigrocarpa</i> R.W. Davidson	<i>Ophiostoma nigrocarpum</i> (R.W. Davidson) de Hoog	<i>Ceratocystis nigrocarpa</i> R.W. Davidson
<i>C. nothofagi</i> Butin	<i>Ophiostoma nothofagi</i> (Butin) Rulamort	<i>Ceratocystis nothofagi</i> Butin
<i>C. novae-zelandiae</i> Hutchison & J. Reid	synonym of <i>Ophiostoma pluriannulatum</i> (Hedgc.) Syd.	<i>Ceratocystis novae-zelandiae</i> Hutchison & J. Reid
<i>C. obscura</i> (R.W. Davidson) J. Hunt	<i>Leptographium obscurum</i> (R.W. Davidson) Z.W. de Beer & M.J. Wingf.	<i>Ceratostomella obscura</i> R.W. Davidson
<i>C. ochracea</i> H.D. Griffin	<i>Ceratocystiopsis ochracea</i> (H.D. Griffin) H.P. Upadhyay	<i>Ceratocystis ochracea</i> H.D. Griffin
<i>C. olivacea</i> (Math.) J. Hunt	<i>Grosmannia olivacea</i> (Math.) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ophiostoma olivaceum</i> Math.
<i>C. olivacepini</i> R.W. Davidson	<i>Grosmannia olivacepini</i> (R.W. Davidson) Z.W. de Beer, Linnakoski & M.J. Wingf.	<i>Ceratocystis olivacepini</i> R.W. Davidson
<i>C. ossiformis</i> Olchow. & J. Reid	synonym of <i>Ophiostoma columnare</i> (Olchow. & J. Reid) Seifert & G. Okada	<i>Ceratocystis ossiformis</i> Olchow. & J. Reid
<i>C. pallida</i> H.D. Griffin	synonym of <i>Ceratocystiopsis minuta-bicolor</i> (R.W. Davidson) H.P. Upadhyay & W.B. Kendr.	<i>Ceratocystis pallida</i> H.D. Griffin
<i>C. pallidobrunnea</i> Olchow. & J. Reid	<i>Ceratocystiopsis pallidobrunnea</i> (Olchow. & J. Reid) H.P. Upadhyay	<i>Ceratocystis pallidobrunnea</i> Olchow. & J. Reid
<i>C. parva</i> Olchow. & J. Reid	<i>Ceratocystiopsis parva</i> (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis parva</i> Olchow. & J. Reid
<i>C. penicillata</i> (Grosmann) C. Moreau	<i>Grosmannia penicillata</i> (Grosmann) Goid.	<i>Ceratostomella penicillata</i> Grosmann
<i>C. perfecta</i> R.W. Davidson	<i>Ophiostoma perfectum</i> (R.W. Davidson) de Hoog	<i>Ceratocystis perfecta</i> R.W. Davidson
<i>C. perparvispora</i> J. Hunt	synonym of <i>Ophiostoma microsporum</i> Arx	<i>Ceratocystis perparvispora</i> J. Hunt
<i>C. piceae</i> (Münch) Bakshi	<i>Ophiostoma piceae</i> (Münch) Syd.	<i>Ceratostomella piceae</i> Münch
<i>C. piceiperda</i> (Rumbold) C. Moreau	<i>Grosmannia piceiperda</i> (Rumbold) Goid.	<i>Ceratostomella piceiperda</i> Rumbold
<i>C. pilifera</i> (Fr.) C. Moreau	<i>Ophiostoma piliferum</i> (Fr. : Fr.) Syd.	<i>Sphaeria pilifera</i> Fr.
<i>C. pini</i> (Münch) C. Moreau	synonym of <i>Ophiostoma minus</i> (Hedgc.) Syd.	<i>Ceratostomella pini</i> Münch
<i>C. pluriannulata</i> (Hedgc.) C. Moreau	<i>Ophiostoma pluriannulatum</i> (Hedgc.) Syd.	<i>Ceratostomella pluriannulata</i> Hedgc.
<i>C. polygrapha</i> Aoshima [<i>nom. inval.</i> , Art. 29.1, 36.1]	synonym of <i>Grosmannia aoshimae</i> (Ohtaka, Masuya & Yamaoka) Masuya & Yamaoka	<i>Ceratocystis polygrapha</i> Aoshima [<i>nom. inval.</i> , Art. 29.1, 36.1]
<i>C. ponderosae</i> T.E. Hinds & R.W. Davidson	synonym of <i>Ophiostoma stenoceras</i> (Robak) Nannf.	<i>Ceratocystis ponderosae</i> T.E. Hinds & R.W. Davidson
<i>C. populicola</i> Olchow. & J. Reid	<i>Ophiostoma populicola</i> (Olchow. & J. Reid) Z.W. de Beer, Seifert, M.J. Wingf.	<i>Ceratocystis populicola</i> Olchow. & J. Reid
<i>C. populina</i> T.E. Hinds & R.W. Davidson	<i>Ophiostoma populinum</i> (T.E. Hinds & R.W. Davidson) de Hoog & Scheffer	<i>Ceratocystis populina</i> T.E. Hinds & R.W. Davidson
<i>C. prolifera</i> Kowalski & Butin	<i>Ophiostoma proliferum</i> (Kowalski & Butin) Rulamort	<i>Ceratocystis prolifera</i> Kowalski & Butin
<i>C. pseudoeurophioides</i> Olchow. & J. Reid	<i>Grosmannia pseudoeurophioides</i> (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis pseudoeurophioides</i> Olchow. & J. Reid
<i>C. pseudominor</i> Olchow. & J. Reid	<i>Ophiostoma pseudominus</i> (Olchow. & J. Reid) Hausner, J. Reid & Klassen	<i>Ceratocystis pseudominor</i> Olchow. & J. Reid
<i>C. pseudonigra</i> Olchow. & J. Reid	<i>Ophiostoma pseudonigrum</i> (Olchow. & J. Reid) Hausner & J. Reid	<i>Ceratocystis pseudonigra</i> Olchow. & J. Reid
<i>C. pseudotsugae</i> (Rumbold) C. Moreau	<i>Ophiostoma pseudotsugae</i> (Rumbold) Arx	<i>Ceratostomella pseudotsugae</i> Rumbold
<i>C. querci</i> (Georgev.) C. Moreau	<i>Ophiostoma quercus</i> (Georgev.) Nannf.	<i>Ceratostomella quercus</i> Georgev.
<i>C. retusi</i> R.W. Davidson & T.E. Hinds	<i>Ophiostoma retusum</i> (R.W. Davidson & T.E. Hinds) Hausner, J. Reid & Klassen	<i>Ceratocystis retusi</i> R.W. Davidson & T.E. Hinds
<i>C. roboris</i> (Georgescu & Teodoru) Potl.	synonym of <i>Ophiostoma quercus</i> (Georgev.) Nannf.	<i>Ophiostoma roboris</i> Georgescu & Teodoru
<i>C. robusta</i> (R.C. Rob. & R.W. Davidson) H.P. Upadhyay	<i>Grosmannia robusta</i> (R.C. Rob. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Europhium robustum</i> R.C. Rob. & R.W. Davidson
<i>C. rostricornata</i> R.W. Davidson & Eslyn	<i>Ophiostoma rostricornatum</i> (R.W. Davidson & Eslyn) de Hoog & Scheffer	<i>Ceratocystis rostricornata</i> R.W. Davidson & Eslyn

(continued on next page)

Table 2. (Continued).

Name in <i>Ceratocystis</i>	Current name	Basionym
<i>C. rostracylindrica</i> (R.W. Davidson) J. Hunt	<i>Leptographium rostracylindricum</i> (R.W. Davidson) Z.W. de Beer & M.J. Wingf.	<i>Ceratostomella rostracylindrica</i> R.W. Davidson
<i>C. sagmatospora</i> E.F. Wright & Cain	<i>Grosmannia sagmatospora</i> (E.F. Wright & Cain) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis sagmatospora</i> E.F. Wright & Cain
<i>C. serpens</i> (Goid.) C. Moreau	<i>Grosmannia serpens</i> Goid.	<i>Grosmannia serpens</i> Goid.
<i>C. shikotsuensis</i> Aoshima [<i>nom. inval.</i> , Art. 29.1, 36.1]	synonym of <i>Grosmannia europhioides</i> (E.F. Wright & Cain) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis shikotsuensis</i> Aoshima [<i>nom. inval.</i> , Art. 29.1, 36.1]
<i>C. sparsa</i> R.W. Davidson	<i>Graphilbum sparsum</i> H.P. Upadhyay & W.B. Kendr.	<i>Ceratocystis sparsa</i> R.W. Davidson
<i>C. spinifera</i> Olchow. & J. Reid	synonym of <i>Ophiostoma fasciatum</i> (Olchow. & J. Reid) Hausner, J. Reid & Klassen	<i>Ceratocystis spinifera</i> Olchow. & J. Reid
<i>C. spinulosa</i> H.D. Griffin	<i>Ceratocystiopsis spinulosa</i> (H.D. Griffin) H.P. Upadhyay	<i>Ceratocystis spinulosa</i> H.D. Griffin
<i>C. stenoceras</i> (Robak) C. Moreau	<i>Ophiostoma stenoceras</i> (Robak) Nannf.	<i>Ceratostomella stenoceras</i> Robak
<i>C. tenella</i> R.W. Davidson	<i>Ophiostoma tenellum</i> (R.W. Davidson) M. Villarreal	<i>Ceratocystis tenella</i> R.W. Davidson
<i>C. tetropii</i> (Math.) J. Hunt	<i>Ophiostoma tetropii</i> Math.	<i>Ceratocystis tetropii</i> (Math.) J. Hunt
<i>C. torticiliata</i> Olchow. & J. Reid	<i>Ophiostoma torticiliata</i> (Olchow. & J. Reid) Seifert & G. Okada	<i>Ceratocystis torticiliata</i> Olchow. & J. Reid
<i>C. torulosa</i> Butin & G. Zimm.	<i>Ophiostoma torulosum</i> (Butin & G. Zimm.) Hausner, J. Reid & Klassen	<i>Ceratocystis torulosa</i> Butin & G. Zimm.
<i>C. tremulo-aurea</i> R.W. Davidson & T.E. Hinds	<i>Ophiostoma tremulo-aureum</i> (R.W. Davidson & T.E. Hinds) de Hoog & Scheffer	<i>Ceratocystis tremulo-aurea</i> R.W. Davidson & T.E. Hinds
<i>C. triangulospora</i> (Butin) H.P. Upadhyay	<i>Ophiostoma triangulosporum</i> Butin	<i>Ophiostoma triangulosporum</i> Butin
<i>C. truncicola</i> (R.W. Davidson) H.D. Griffin	<i>Grosmannia truncicola</i> (R.W. Davidson) Z.W. de Beer & M.J. Wingf.	<i>Ophiostoma truncicola</i> R.W. Davidson
<i>C. tubicollis</i> Olchow. & J. Reid	<i>Graphilbum tubicolle</i> (Olchow. & J. Reid) Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis tubicollis</i> Olchow. & J. Reid
<i>C. ulmi</i> (Buisman) C. Moreau	<i>Ophiostoma ulmi</i> (Buisman) Nannf.	<i>Ceratostomella ulmi</i> Buisman
<i>C. valachicum</i> (Georgescu, Teodoru & Badea) Potl.	<i>Ophiostoma valachicum</i> Georgescu, Teodoru & Badea	<i>Ophiostoma valachicum</i> Georgescu, Teodoru & Badea
<i>C. vesca</i> R.W. Davidson	<i>Grosmannia vesca</i> (R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis vesca</i> R.W. Davidson
<i>C. wagneri</i> Goheen & F.W. Cobb	<i>Grosmannia wagneri</i> (Goheen & F.W. Cobb) Zipfel, Z.W. de Beer & M.J. Wingf.	<i>Ceratocystis wagneri</i> Goheen & F.W. Cobb

Descriptions: Von Arx & Hennebert (1965: 312–315, fig. 2); Batra (1967: 990–992, figs 14–19).

Notes: Sexual state unknown. The genus and species were invalidly described by Brader (1964) (Art. 40.1), but Von Arx & Hennebert (1965) redescribed and validated both.

***Ceratocystis* Ellis & Halst., In: Halsted, New Jersey Agric. Coll. Exp. Sta. Bull. 76: 14. 1890.**

?= *Rostrella* Zimm., Meded. Lands Plantentuin, Batavia 37: 24. 1900. (*nom. illegit.*, Art. 53.1, later homonym for *Rostrella* Fabre, Ann. Sci. Nat., Bot. 6, 9: 66. 1879) (type species *Ro. coffeae*).
= *Ceratocystis* Ellis & Halst. section *Ceratocystis* pro parte, In: Upadhyay, *Monogr. Ceratocystis & Ceratocystiopsis*: 32. 1981.

Type species: *Ceratocystis fimbriata* Ellis & Halst., New Jersey Agric. Coll. Exp. Sta. Bull. 76: 14. 1890.

Emended generic diagnosis. *Ascomatal* bases globose, brown to black, unornamented or with undifferentiated ornamental hyphae. *Ascomatal* necks long, tapering to apex, straight, dark-brown to black, hyaline at apex. *Ostiolar* hyphae divergent, non-septate, tapered, light brown to hyaline. *Asci* dehiscent. *Ascospores* one-celled, hat-shaped, hyaline, accumulating in cream-coloured masses at tips of necks. *Primary conidiophores* phialidic, flask-

shaped. *Secondary conidiophores* flaring or wide-mouthed. *Primary conidia* cylindrical, hyaline. *Secondary conidia* barrel to subglobose shaped, hyaline to light brown. *Aleurioconidia* globose, ovoid to pyriform, singly or in chains, pale-brown to brown.

Notes: The most characteristic features of this genus are the ascomatal bases lacking distinct ornamentations and hat-shaped ascospores. The possibility that *Ro. coffeae* might not be a synonym of *C. fimbriata* is discussed under the latter species, below. However, even if the two species are distinct, the species from coffee would probably still group in *Ceratocystis* s. str., which means *Rostrella* will remain a synonym of *Ceratocystis*.

***Ceratocystis acaciivora* Tarigan & M. van Wyk, S. Afr. J. Bot. 77: 301. 2011.**

***Ceratocystis albifundus* M.J. Wingf., De Beer & M.J. Morris, Syst. Appl. Microbiol. 19: 196. 1996. (as “*albofundus*”).**

***Ceratocystis atrox* M. van Wyk & M.J. Wingf., Australas. Pl. Pathol. 36: 411. 2007.**

Table 3. Species previously treated in *Ceratocystis* s.l. but that can be excluded from the current generic concepts based on morphology. However, the correct generic placement of these species remains uncertain and in need of confirmation with DNA sequences. More details on each species are presented by De Beer *et al.* (2013b).

Name in <i>Ceratocystis</i>	Basionym	Probable ordinal, generic placement
<i>C. acericola</i> H.D. Griffin	<i>Ceratocystis acericola</i> H.D. Griffin	Ophiostomatales, <i>Ophiostoma</i> s.l. or <i>Leptographium</i> s.l.
<i>C. acoma</i> (V.V. Miller & Cernzow) C. Moreau	<i>Ceratostomella acoma</i> V.V. Miller & Cernzow	Ophiostomatales, <i>Ophiostoma</i> s. str.
<i>C. aequivaginata</i> Olchow. & J. Reid	<i>Ceratocystis aequivaginata</i> Olchow. & J. Reid	Ophiostomatales, <i>Leptographium</i> s.l.
<i>C. alba</i> DeVay, R.W. Davidson & W.J. Moller	<i>Ceratocystis alba</i> DeVay, R.W. Davidson & W.J. Moller	Peripheral to Ophiostomatales
<i>C. autographa</i> Bakshi	<i>Ceratocystis autographa</i> Bakshi	Sordariomycetidae, <i>incertae sedis</i>
<i>C. brevicollis</i> R.W. Davidson	<i>Ceratocystis brevicollis</i> R.W. Davidson	Ophiostomatales, <i>Ophiostoma</i> s.l. or <i>Leptographium</i> s.l.
<i>C. buxi</i> (Borissov) C. Moreau	<i>Ceratostomella buxi</i> Borissov	Sordariomycetidae, <i>incertae sedis</i> , <i>Ceratostomella</i>
<i>C. comata</i> (V.V. Miller & Cernzow) C. Moreau	<i>Ceratostomella comata</i> V.V. Miller & Cernzow	Ophiostomatales, <i>Leptographium</i> s.l.
<i>C. deltoideospora</i> Olchow. & J. Reid	<i>Ceratocystis deltoideospora</i> Olchow. & J. Reid	Ophiostomatales, <i>Raffaelea</i>
<i>C. grandicarpa</i> Kowalski & Butin	<i>Ceratocystis grandicarpa</i> Kowalski & Butin	Ophiostomatales, genus uncertain
<i>C. imperfecta</i> (V.V. Miller & Cernzow) C. Moreau	<i>Ceratostomella imperfecta</i> V.V. Miller & Cernzow	Ophiostomatales, <i>Leptographium</i> s.l.
<i>C. magnifica</i> H.D. Griffin	<i>Ceratocystis magnifica</i> H.D. Griffin	Ophiostomatales, <i>Ophiostoma</i> s.l.
<i>C. merolinensis</i> (Georgev.) C. Moreau	<i>Ceratostomella merolinensis</i> Georgev.	Sordariomycetidae, <i>incertae sedis</i> , <i>Ceratostomella</i>
<i>C. microcarpa</i> (P. Karst.) C. Moreau	<i>Ceratostomella microcarpa</i> P. Karst.	Sordariomycetidae, <i>incertae sedis</i> , <i>Ceratostomella</i>
<i>C. seticollis</i> R.W. Davidson	<i>Ceratocystis seticollis</i> R.W. Davidson	Ophiostomatales, genus uncertain
<i>C. stenospora</i> H.D. Griffin	<i>Ceratocystis stenospora</i> H.D. Griffin	Ophiostomatales, <i>Ophiostoma</i> s.l. or <i>Leptographium</i> s.l.
<i>C. trinacriformis</i> (A.K. Parker) H.P. Upadhyay	<i>Europhium trinacriforme</i> A.K. Parker	Ophiostomatales, <i>Ophiostoma</i> s.l. or <i>Leptographium</i> s.l.
<i>C. valdiviana</i> Butin	<i>Ceratocystis valdiviana</i> Butin	Ophiostomatales, <i>Leptographium</i> s.l.

Ceratocystis cacaofunesta Engelbr. & T.C. Harr., Mycologia 97: 64. 2005.

Note: In earlier studies this species was treated as residing in the Latin American “cacao” population of *C. fimbriata* (Baker Engelbrecht *et al.* 2003).

Ceratocystis caryae J.A. Johnson & T.C. Harr., Mycologia 97: 1086. 2005.

Ceratocystis colombiana M. van Wyk & M.J. Wingf., Fungal Diversity 40: 111. 2010.

Table 4. Species described invalidly in *Ceratocystis*, but for which validation is possible. More details on each species are presented by De Beer *et al.* (2013b).

Name in <i>Ceratocystis</i>	Basionym	Reason for invalidity
² <i>C. antennaroidospora</i> Roldan	<i>Ceratocystis antennaroidospora</i> Roldan	Art. 40.1
² <i>C. asteroides</i> Roldan	<i>Ceratocystis asteroides</i> Roldan	Art. 40.1
¹ <i>C. chinensis</i> G.H. Zhao	<i>Ceratocystis chinensis</i> G.H. Zhao	Art. 40.1, 40.6
² <i>C. heveae</i> G.H. Zhao	<i>Ceratocystis heveae</i> G.H. Zhao	Art. 40.6
² <i>C. jezoensis</i> Aoshima	<i>Ceratocystis jezoensis</i> Aoshima	Art. 29.1 & 36.1
¹ <i>C. kubanica</i> (Sczerbin-Parfenenko) Pottlajchuk	<i>Ophiostoma kubanicum</i> Sczerbin-Parfenenko	Art. 36.1
¹ <i>C. minor</i> (Hedgc.) J. Hunt var. <i>barrasii</i> J.J. Taylor	<i>Ceratocystis minor</i> (Hedgc.) J. Hunt var. <i>barrasii</i> J.J. Taylor	Art. 40.1
² <i>C. pidoplichikovii</i> Milko	<i>Ceratocystis pidoplichikovii</i> Milko	Art. 40.1
² <i>Thielaviopsis wallemiiiformis</i> Dominik & Ihnat.	<i>Thielaviopsis wallemiiiformis</i> Dominik & Ihnat.	Art. 40.1

¹ Species that most likely belong in the Ophiostomatales and to be excluded from *Ceratocystis* s.l. upon validation.

² Species that have thielaviopsis-like asexual states and probably belong to genera in the *Ceratocystidaceae*.

Table 5. Species names from the invertebrate fossil genus, *Ceratocystis* Jaekel (*Echinodermata*, *Stylophora*). Although the application of these names to fungal species are permissible because they are dictated by a different nomenclatural Code, their use should preferably be avoided (De Beer *et al.* 2013a).

Species

Ceratocystis perneri Jaekel

Ceratocystis prosthakida Rahman, Zamora & Geyer

Ceratocystis spinosa Ubaghs

Ceratocystis vizcainoi Ubaghs

Ceratocystis corymbicola Kamgan & Jol. Roux, *Antonie van Leeuwenhoek* 101: 237. 2012.

Ceratocystis curvata M. van Wyk & M.J. Wingf., *Fungal Diversity* 46: 122. 2011.

Ceratocystis diversiconidia M. van Wyk & M.J. Wingf., *Fungal Diversity* 46: 125. 2011.

Ceratocystis ecuadoriana M. van Wyk & M.J. Wingf., *Fungal Diversity* 46: 122. 2011.

Ceratocystis eucalypticola M. van Wyk & M.J. Wingf., *IMA Fungus* 3: 54. 2012.

Ceratocystis ficicola Kajitani & Masuya, *Mycoscience* 52: 351. 2011.

Ceratocystis fimbriata Ellis & Halst., *New Jersey Agric. Coll. Exp. Sta. Bull.* 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., *Svenska Skogsv. Fören. Tidskr.* 32: 408. 1934.

≡ *Endoconidiophora fimbriata* (Ellis & Halst.) R.W. Davidson, *J. Agric. Res.* 50: 800. 1935.

?= *Rostrella coffeae* Zimm., *Meded. Lands Plantentuin, Batavia* 37: 32. 1900.

≡ *Ophiostoma coffeae* (Zimm.) Arx, *Antonie van Leeuwenhoek* 18: 210. 1952.

≡ *Ceratocystis moniliformis* f. *coffeae* (Zimm.) C. Moreau, *Bull. Sci. Minist. France Outre-Mer* 5: 424. 1954.

Descriptions: Davidson (1935: 799–800); Hunt (1956: 11–16); Webster & Butler (1967: 1459–1463, pl. I–VI); Griffin (1968: 703); Morgan-Jones (1967a, figs A–G); Olchowicki & Reid (1974: 1699, pl. XIII, fig. 258); Matsushima (1975: 169, pl. 382, 383); Nag Raj & Kendrick (1975: 118, 141, fig. 45); Upadhyay (1981: 44, figs 69–72); Potlajczuk & Schekunova (1985: 150); Engelbrecht & Harrington (2005: 63–64).

Notes: The original description of *Ceratocystis fimbriata* was from sweet potato in the USA. Analyses of DNA sequences have shown that the fungus treated as *C. fimbriata* in various studies and from various countries and host plants, represent a species complex that includes many different cryptic species (Van Wyk

et al. 2013). The name *C. fimbriata* should be restricted to the fungus from sweet potato and to other isolates belonging to the same phylogenetic species.

Pontis (1951) listed *Rostrella coffeae* as a synonym of *C. fimbriata*, but mentioned biological differences between isolates from the coffee tree and sweet potato. Several recent studies, based on DNA sequence comparisons for multiple gene regions, have distinguished host-specific and geographically-separated populations, including populations from coffee, in the *C. fimbriata* species complex (Harrington 2000, Barnes *et al.* 2001, 2003, Baker Engelbrecht *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 from coffee in Colombia as new species, but did not 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 present we treat *R. coffeae* as a synonym of *C. fimbriata* until future studies with fresh isolates from coffee in Java provide further insights into this question.

Ceratocystis fimbriatomima M. van Wyk & M.J. Wingf., *Fungal Diversity* 34: 180. 2009.

Ceratocystis harringtonii Z.W. de Beer & M.J. Wingf., *CBS Biodiversity Series* 12: 291. 2013.

≡ *Ceratocystis populicola* J.A. Johnson & T.C. Harr., *Mycologia* 97: 1084. 2005. (nom. illegit., Art 53.1).

Notes: Johnson *et al.* (2005) described this species validly, but the name was a later homonym for *Ceratocystis populicola* Olchow. & J. Reid (= *Ophiostoma populicola*) and thus illegitimate. De Beer *et al.* (2013b) provided a new, legitimate name.

Ceratocystis larium M. van Wyk & M.J. Wingf., *Persoonia* 22: 80. 2009.

Ceratocystis mangicola M. van Wyk & M.J. Wingf., *Mycotaxon* 117: 395. 2011.

Ceratocystis manginecans M. van Wyk, Al Adawi & M.J. Wingf., *Fungal Diversity* 27: 224. 2007.

Ceratocystis mangivora M. van Wyk & M.J. Wingf., *Mycotaxon* 117: 397. 2011.

Ceratocystis neglecta M. van Wyk, Jol. Roux & C. Rodas, *Fungal Diversity* 28: 80. 2008.

Ceratocystis obpyriformis R.N. Heath & Jol. Roux, *Fungal Diversity* 34: 57. 2009.

Ceratocystis papillata M. van Wyk & M.J. Wingf., *Fungal Diversity* 40: 112. 2010.

Ceratocystis pirilliformis I. Barnes & M. J. Wingf., *Mycologia* 95: 867. 2003.

= *Ceratocystis zombamontana* R.N. Heath & Jol. Roux, *Fungal Diversity* 34: 53. 2009.

Note: Kamgan Nkuekam *et al.* (2012) showed *C. zombamontana* to be a synonym of *C. pirilliformis* based on DNA sequence data.

Ceratocystis platani (Walter) Engelbr. & T.C. Harr., *Mycologia* 97: 65. 2005.

Basionym: *Endoconidiophora fimbriata* f. *platani* Walter, *Phytopathology* 42: 236. 1952.

Note: This species was considered to represent a population of *C. fimbriata* from sycamore (*Platanus*) (Santini & Capretti 2000, Barnes *et al.* 2001, Baker Engelbrecht *et al.* 2003, Engelbrecht *et al.* 2004, Thorpe *et al.* 2005), until Engelbrecht & Harrington (2005) elevated it to species level.

Ceratocystis polychroma M. van Wyk, M.J. Wingf. & E.C.Y. Liew, *Stud. Mycol.* 50, 278. 2004.

Ceratocystis polyconidia R.N. Heath & Jol. Roux, *Fungal Diversity* 34: 53. 2009.

Ceratocystis smalleyi J.A. Johnson & T.C. Harr., *Mycologia* 97: 1088. 2005.

Ceratocystis tanganyicensis R.N. Heath & Jol. Roux, *Fungal Diversity* 34: 56. 2009.

Ceratocystis thulamensis M. Mbenoun & Jol. Roux, *Mycol. Progress* 13: 234. 2014.

Ceratocystis tsitsikammensis Kamgan & Jol. Roux, *Fungal Diversity* 29: 50. 2008.

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.

Basionym: *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. 39.1).

Descriptions: Hunt (1956: 16–18); Johnson *et al.* (2005: 1082–1084, figs 8–16).

Notes: *Ceratocystis variospora* was invalidly reduced to a *forma* of *C. moniliformis* by Moreau (1952). Webster & Butler (1967), Upadhyay (1981), and Seifert *et al.* (1993) all treated *C. variospora* as synonym of *C. fimbriata*. Johnson *et al.* (2005) re-instated it as a distinct species in the *C. fimbriata* complex based on phylogenetic analyses.

Ceratocystis zambeziensis M. Mbenoun & Jol. Roux, *Mycol. Progress* 13: 235. 2014.

Chalaropsis Peyronel, *Le Staz. Sper. agric.* 49: 595. 1916.

Type species: *Chalaropsis thielavioides* Peyronel, *Le Staz. Sper. agric.* 49: 58. 1916.

Emended generic diagnosis. *Sexual state* not observed. *Conidiophores* arise laterally from vegetative hyphae. *Conidiogenous cells* phialidic, cylindrical, tapering toward apex,

hyaline, subhyaline or pale brown. *Conidia* unicellular, cylindrical with rounded or truncate ends, hyaline to light brown, singly or in chains. *Aleurioconidia* unicellular, globose, ellipsoidal, ovoid, or pyriform with truncate ends, solitary and terminal on sympodially branching conidiophores, pale brown to brown.

Note: The morphological characters of *Chalaropsis* species are indistinguishable from those of the asexual states of *Ceratocystis* s. *str.*

Chalaropsis ovoidea (Nag Raj & W.B. Kendr.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810308.

Basionym: *Chalara ovoidea* Nag Raj & W.B. Kendr., *Monogr. Chalara*: 127. 1975.

≡ *Thielaviopsis ovoidea* (Nag Raj & W.B. Kendr.) A.E. Paulin, T.C. Harr. & McNew, *Mycologia* 94: 70. 2002.

Description: Nag Raj & Kendrick (1975: 116, 127–128, figs 43B).

Notes: Two isolates of this species were included in our analyses, none of which represented the type. Epitypification of this name is needed.

Chalaropsis populi (Kiffer & Delon) Z.W. de Beer, T.A. Duong & M.J. Wingf. **comb. nov.**

Basionym: *Chalara populi* Kiffer & Delon, *Mycotaxon* 18: 171. 1983. (as “Veldeman ex”).

≡ *Thielaviopsis populi* (Kiffer & Delon) A.E. Paulin, T.C. Harr. & McNew, *Mycologia* 94: 70. 2002.

= *Chalaropsis populi* Veldeman, *Meded. Fac. Landbouwwetensch. Rijksuniv. Gent* 36: 1001. 1971. (nom. inval., Art. 39.1, 40.1).

Description: Kiffer & Delon (1983: 171–172, figs 1–2).

Notes: Veldeman (1971) did not provide a formal diagnosis in the description of this species. Kiffer & Delon (1983) studied the original material and validated the name. No isolates representing *Chalaropsis populi* were available for the present study, but sequence data from previous studies confirm its placement in this genus (Wingfield *et al.* 2013).

***Chalaropsis* sp. 1**

Note: Two isolates included in this study that had been labelled as *T. thielavioides* in the CBS collection, emerged as representing an undescribed species in this genus, distinct from *Chalaropsis thielavioides*.

Chalaropsis thielavioides Peyronel, *Le Staz. Sper. agric.* 49: 58. 1916.

≡ *Chalara thielavioides* (Peyronel) Nag Raj & W.B. Kendr., *Monogr. Chalara*: 136. 1975.

≡ *Thielaviopsis thielavioides* (Peyronel) A.E. Paulin, T.C. Harr. & McNew, *Mycologia* 94: 70. 2002.

= *Chalaropsis thielavioides* Peyronel var. *ramosissima* Sugiyama, *J. Fac. Sci. Univ. Tokyo* 10: 33. 1968.

Description: Nag Raj & Kendrick (1975: 117, 136–137, fig. 44).

Note: Nag Raj & Kendrick (1975) considered *Ch. thielavioides* var. *ramosissima* a synonym of *Ch. thielavioides*.

Davidsoniella Z.W. de Beer, T.A. Duong & M.J. Wingf., **gen. nov.** MycoBank MB810235.

Etymology: Named after Ross Wallace Davidson who described at least 41 ophiostomatoid species during his career at the USDA. These included *Ceratocystis virescens*, the type species for this new genus.

Type species: *Davidsoniella virescens* (R.W. Davidson) Z.W. de Beer, T.A. Duong & M.J. Wingf.

Ascomatal bases globose, light brown to dark brown to black, ornamental hyphae, simple, septate, stiff. *Ascomatal necks* long, dark brown at base to light brown at apex. *Ostiolar hyphae* divergent to straight, non-septate, smooth, light brown to hyaline. *Asci* dehiscent. *Ascospores* one-celled, elongate, narrow fusiform to spindle shaped, slightly curved, with thick, hyaline sheath. *Conidiophores* arise laterally from vegetative hyphae. *Conidiogenous cells* phialidic, cylindrical, hyaline. *Conidia* unicellular, cylindrical with flattened ends, barrel-shaped, hyaline, borne in chains of varying length. *Aleuriiconidia* not present.

Note: The most distinctive features of this genus are elongated, spindle-shaped and sheathed ascospores that are substantially longer than those of *Endoconidiophora* spp.

Davidsoniella australis (J. Walker & Kile) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810241.

Basionym: *Chalara australis* J. Walker & Kile, Austral. J. Bot. 35: 7. 1987. (non *Chalara australis* McKenzie, Mycotaxon 46: 291 (1993), nom. illegit.).

≡ *Thielaviopsis australis* (J. Walker & Kile) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 69. 2002.

Note: Sexual state unknown.

Davidsoniella eucalypti (Z.Q. Yuan & Kile) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810309.

Basionym: *Ceratocystis eucalypti* Z.Q. Yuan & Kile, Mycol. Res. 100: 573. 1996.

≡ *Chalara eucalypti* Z.Q. Yuan & Kile, Mycol. Res. 100: 573. 1996.
≡ *Thielaviopsis eucalypti* (Z.Q. Yuan & Kile) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 69. 2002.

Davidsoniella neocaledoniae (Kiffer & Delon) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810310.

Basionym: *Chalara neocaledoniae* Dadant ex Kiffer & Delon, Mycotaxon 18: 166. 1983.

≡ *Thielaviopsis neocaledoniae* (Kiffer & Delon) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 70. 2002.
= *Thielaviopsis neocaledoniae* Dadant, Rev. Gén. Bot. 57: 176. 1950. (nom. inval., Art. 39.1).

Description: Kiffer & Delon (1983): 166–170, figs 1–2).

Notes: Sexual state unknown. Dadant (1950) did not provide a Latin diagnosis and also failed to designate a type specimen, making the species name invalid. Kiffer & Delon (1983) obtained the original isolate of Dadant and validated the name.

Davidsoniella virescens (R.W. Davidson) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810311.

Basionym: *Endoconidiophora virescens* R.W. Davidson, Mycologia 36: 301. 1944.

≡ *Ceratocystis virescens* (R.W. Davidson) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.

≡ *Ophiostoma virescens* (R.W. Davidson) Arx, Antonie van Leeuwenhoek 18: 212. 1952.

Description: Samuels (1993): 16, figs 1A–B).

Notes: Hunt (1956), Olchowecki & Reid (1974), and Upadhyay (1981) treated *C. virescens* as a synonym of *C. coerulescens*, but Nag Raj & Kendrick (1975), Gibbs (1993), Kile (1993), and Seifert *et al.* (1993), considered the two species distinct. Witthuhn *et al.* (1998) confirmed the separateness of the species.

Endoconidiophora Münch, Naturw. Z. Forst- u. Landw. 5: 564. 1907.

= *Ceratocystis* Ellis & Halst. section *Endoconidiophora* (Münch) H.P. Upadhyay pro parte, In: Upadhyay, Monogr. *Ceratocystis* & *Ceratocystiopsis*: 64. 1981.

Type species: *Endoconidiophora coerulescens* Münch, Naturw. Z. Forst- u. Landw. 5: 564. 1907.

Emended generic diagnosis. *Ascomatal bases* globose to ovoid, dark brown, with distinct basal spines. *Ascomatal necks* long, tapering towards apex, dark brown to black. *Ostiolar hyphae* divergent, non-septate, hyaline. *Asci* dehiscent. *Ascospores* one-celled, elongate to slightly curved with round ends, oblong cylindrical, surrounded by distinct translucent sheath. *Conidiophores* tubular, rectangular, cylindrical, sometimes slightly flared collarette. *Conidiogenous cells* phialidic, oblong cylindrical. *Conidia* unicellular, rectangular with two attachment points, hyaline, in chains. *Aleuriiconidia* not present.

Note: The most distinctive features of this genus are the long spines on the ascomatal bases and the sheathed ascospores (see Harrington & Wingfield 1998)

Endoconidiophora coerulescens Münch, Naturw. Z. Land. Forstw. 5: 564. 1907.

≡ *Ceratocystis coerulescens* (Münch) Bakshi, Trans. Br. Mycol. Soc. 33: 114. 1950. emend. T.C. Harr. & M.J. Wingf., Canad. J. Bot. 76: 1448. 1998.

≡ *Ophiostoma coerulescens* (Münch) Nannf., Svenska Skogsv.-Fören. 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.

Descriptions: Lagerberg *et al.* (1927): 196–203, figs 22–26); Davidson (1935): 798–799); Siemaszko (1939): 20–22, pl. I, figs 9–13); Bakshi (1951): 2–5); Hunt (1956): 17, 21–23); Griffin (1968): 700–701); Nag Raj & Kendrick (1975): 94, 138–139, fig. 32B); Upadhyay (1981): 65, figs 191–196); Potlajczuk & Schekunova (1985): 149–150); Harrington & Wingfield (1998): 1448–1449).

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) and Paulin-Mahady *et al.* (2002) accepted the suggestion by Münch (1907) that *Ca. ungeri* represented the asexual state of *C. coerulescens*. In the absence of an ex-type culture representing *Ca. ungeri*, the synonymy can neither be confirmed nor rejected. 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).

Endoconidiophora douglasii (R.W. Davidson) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810312.

Basionym: *Endoconidiophora coerulescens* f. *douglasii* R.W. Davidson, Mycologia 45: 584. 1953.

≡ *Ceratocystis douglasii* (R.W. Davidson) M.J. Wingf. & T.C. Harr., Canad. J. Bot. 75: 832. 1997

Notes: Upadhyay (1981) considered *Endoconidiophora coerulescens* f. *douglasii* a synonym of *C. coerulescens*. Wingfield *et al.* (1997) distinguished *C. coerulescens* from *C. douglasii* and elevated the latter to species level.

Endoconidiophora fujiensis (M.J. Wingf., Yamaoka & Marin) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810313.

Basionym: *Ceratocystis fujiensis* M.J. Wingf., Yamaoka & Marin, Mycol. Res. 109: 1142. 2005.

Endoconidiophora laricicola (Redfern & Minter) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810314.

Basionym: *Ceratocystis laricicola* Redfern & Minter, Pl. Pathol. 36: 468. 1987.

Descriptions: Harrington & Wingfield (1998: 1453, 1456); Yamaoka *et al.* (1998: 369–371, figs 6–10); Marin *et al.* (2005: 1142, 1144).

Note: Witthuhn *et al.* (2000) and Harrington *et al.* (2002) distinguished *C. laricicola* from the morphologically similar *C. polonica* based on differences in bark beetle associates, conifer hosts and molecular data.

Endoconidiophora pinicola (T.C. Harr. & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810315.

Basionym: *Ceratocystis pinicola* T.C. Harr. & M.J. Wingf., Canad. J. Bot. 76: 1452. 1998.

Endoconidiophora polonica (Siemaszko) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810316.

Basionym: *Ophiostoma polonicum* Siemaszko, Planta Pol. 7: 32. 1939.

≡ *Ceratocystis polonica* (Siemaszko) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952. emend. T.C. Harr. & M.J. Wingf., Canad. J. Bot. 76(8): 1452. 1998. (as "*polonicum*").

Descriptions: Siemaszko (1939: 20, 32–33, pl. IV, figs 1–10); Mathiesen (1951: 208–210); Hunt (1956: 27); Solheim (1986:

205–206); Yamaoka *et al.* (1997: 1217–1219); Harrington & Wingfield (1998: 1452–1453, 1455); Marin *et al.* (2005: 1142, 1144).

Notes: Siemaszko (1939) erroneously linked a leptographium-like asexual state to *O. polonicum*. Upadhyay (1981) therefore treated the species as a synonym of *O. penicillatum*. However, Solheim (1986) and Harrington (1988) distinguished the two species. Visser *et al.* (1995) confirmed the placement of the species in *Ceratocystis* based on DNA sequence data. Harrington & Wingfield (1998) designated a neotype. *Ceratocystis polonica* was distinguished from the morphologically similar *C. laricicola* by Witthuhn *et al.* (2000) and Harrington *et al.* (2002), based primarily on differences in conifer hosts and bark beetle associates. Marin *et al.* (2009) showed that European and Japanese populations of *C. polonica* are genetically isolated and possibly in the process of speciation.

Endoconidiophora resinifera (T.C. Harr. & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810337.

Basionym: *Ceratocystis resinifera* T.C. Harr. & M.J. Wingf., Canad. J. Bot. 76: 1449. 1998.

Endoconidiophora rufipennis (M.J. Wingf., T.C. Harr. & H. Solheim) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810317.

Basionym: *Ceratocystis rufipennis* M.J. Wingf., T.C. Harr. & H. Solheim, Canad. J. Bot. 75: 828. 1997. (as "*rufipenni*").

Huntella Z.W. de Beer, T.A. Duong & M.J. Wingf., **gen. nov.** MycoBank MB810236.

Etymology: Named after the late John Hunt, author of the monograph of *Ceratocystis* that was published in 1956 (Hunt 1956) and in honour of the major contribution he made to the taxonomy of this group of fungi during his short career.

Type species: *Huntella moniliformis* (Hedgc.) Z.W. de Beer, T.A. Duong & M.J. Wingf.

Ascomatal bases globose to pyriform, black, ornamented with dark brown to black, conical spines, occasionally septate. *Ascomatal necks* long, tapering to apex, black, with a disk-like base. *Ostiolar hyphae* convergent to divergent, hyaline. *Asci* dehiscent. *Ascospores* one-celled, hat-shaped, hyaline. *Primary conidiophores* phialidic, long, septate, tapering to tip. *Secondary conidiophores* phialidic, short, septate. *Primary conidia* cylindrical, truncate ends, hyaline, in long chains. *Secondary conidia* barrel-shaped, hyaline to pale brown. *Aleurioconidia* not observed.

Note: The most distinctive features of this genus are the conical spines on the ascomatal bases, the disk-like bases of the ascomatal necks, and the hat-shaped ascospores.

Huntella bhutanensis (M. van Wyk, M.J. Wingf. & T. Kirisits) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810318.

Basionym: *Ceratocystis bhutanensis* M. van Wyk, M.J. Wingf. & T. Kirisits, Stud. Mycol. 50: 373. 2004.

Note: This is an unusual taxon because it is the only species associated with a bark beetle, *Ips smutzenhoferi*, that infests *Pinus wallichiana* in Bhutan (Kirisits *et al.* 2013).

Huntiella ceramica (R.N. Heath & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810319.

Basionym: *Thielaviopsis ceramica* R.N. Heath & Jol. Roux, Fungal Diversity 34: 60.

Note: Sexual state unknown.

Huntiella chinaeucensis (S.F. Chen, M. van Wyk, M.J. Wingf. & X.D. Zhou) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810320.

Basionym: *Ceratocystis chinaeucensis* S.F. Chen, M. van Wyk, M.J. Wingf. & X.D. Zhou, Fungal Diversity 58: 274. 2013.

Huntiella cryptoformis (Mbenoun & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810321.

Basionym: *Ceratocystis cryptoformis* Mbenoun & Jol. Roux, Mycol. Progress 13: 232. 2014.

Note: Although an isolate of this species was not included in the present study, DNA sequences generated by Mbenoun *et al.* (2014b) undoubtedly place this species in *Huntiella*.

Huntiella decipiens (Kamgan & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810322.

Basionym: *Ceratocystis decipiens* Kamgan & Jol. Roux, Austral. Pl. Pathol. 42: 299. 2013.

Huntiella inquinans (Tarigan, M. van Wyk & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf. **comb. nov.** MycoBank MB810323.

Basionym: *Ceratocystis inquinans* Tarigan, M. van Wyk & M.J. Wingf., Mycoscience 51: 58. 2010.

Huntiella microbasis (Tarigan, M. van Wyk & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810324.

Basionym: *Ceratocystis microbasis* Tarigan, M. van Wyk & M.J. Wingf., Mycoscience 51: 61. 2010.

Huntiella moniliformis (Hedgc.) Z.W. de Beer, T.A. Duong & M.J. Wingf. **comb. nov.** MycoBank MB810325.

Basionym: *Ceratostomella moniliformis* Hedgc., Annual Rep. Missouri Bot. Gard. 17: 78. 1906.

≡ *Ophiostoma moniliforme* (Hedgc.) Syd., In Sydow & Sydow, Ann. 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).

≡ *Ceratocystis moniliformis* (Hedgc.) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.

= *Endoconidiophora bunae* Kitajima, Bull. Imp. Forest Exp. Sta. 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 "wilsonii").

≡ *Ceratocystis moniliformis* f. *wilsonii* C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 23. 1952. (as "wilsonii"; nom. inval., Art. 39.1).

= *Ophiostoma moniliforme* f. *davidsonii* Luc, Rev. Mycol. (Paris) Suppl. Col. 17: 12. 1952. (nom. inval., Art. 39.1).

= *Ophiostoma moniliforme* f. *pycnanthi* Luc, Rev. Mycol. (Paris) Suppl. Col. 17: 12. 1952. (nom. inval., Art. 39.1).

= *Ophiostoma moniliforme* f. *typica* Luc, Rev. Mycol. (Paris) Suppl. Col. 17: 12. 1952. (nom. inval., Art. 24.3 & Art. 39.1).

= *Ophiostoma moniliforme* f. *theobromae* Luc, Rev. Mycol. (Paris) Suppl. Col. 17: 13. 1952. (nom. inval., Art. 39.1).

= *Ceratocystis filiformis* Roldan, Philipp. J. Sci. 91: 418. 1962.

Descriptions: Hedgcock (1906: 78–80, pl. 3, fig. 5, pl. 5, figs 3–5); Davidson (1935: 799–800); Moreau & Moreau (1952, figs 1–4); Luc (1952: 12–15, figs 1–2); Hunt (1956: 13, 17–19); Morgan-Jones (1967b, figs A–H); Nag Raj & Kendrick (1975: 116, 141–142, fig. 43A); Upadhyay (1981: 51, figs 109–115); Maekawa *et al.* (1987: 8–10, figs 7–18); Kowalski & Butin (1989: 238–241).

Notes: Four varieties were described invalidly for *C. moniliformis* by Luc (1952). Moreau (1952) then reduced two species, *C. wilsonii* and *C. variopora* (now considered a distinct species), to *formae* of *C. moniliformis*, and treated *R. coffeae* as a synonym (see notes above under *C. fimbriata*). Moreau & Moreau (1952) reduced *O. moniliforme* f. *theobromae* to synonymy with *C. moniliformis*, and Hunt (1956) did the same with *E. bunae* and *C. wilsonii*. Nag Raj & Kendrick (1975) and Upadhyay (1981) added *C. filiformis* to the synonyms of *C. moniliformis*. The accuracy of all these synonymies deserves to be carefully reconsidered based on DNA sequence data and fresh isolates obtained from similar hosts.

Huntiella moniliformopsis (Yuan & Mohammed) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810326.

Basionym: *Ceratocystis moniliformopsis* Yuan & Mohammed, Austral. Syst. Bot. 15: 126. 2002.

Huntiella oblonga (R.N. Heath & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810328.

Basionym: *Ceratocystis oblonga* R.N. Heath & Jol. Roux, Fungal Diversity 34: 59. 2009.

Huntiella omanensis (Al-Subhi, M.J. Wingf., M. van Wyk & Deadman) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810329.

Basionym: *Ceratocystis omanensis* Al-Subhi, M.J. Wingf., M. van Wyk & Deadman, Mycol. Res. 110: 242. 2006.

Huntiella salinaria (Kamgan & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810330.

Basionym: *Ceratocystis salinaria* Kamgan & Jol. Roux, Austral. Pl. Pathol. 42: 298. 2013.

Huntiella savannae (Kamgan & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810331.

Basionym: *Ceratocystis savannae* Kamgan & Jol. Roux, Fungal Diversity 29: 52. 2008.

Huntiella sublaevis (M. van Wyk & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810332.

Basionym: *Ceratocystis sublaevis* M. van Wyk & M.J. Wingf., Fungal Diversity 46: 128. 2011.

Huntiella sumatrana (Tarigan, M. van Wyk & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810333.

Basionym: *Ceratocystis sumatrana* Tarigan, M. van Wyk & M.J. Wingf., Mycoscience 51: 60. 2010.

Huntiella tribiliformis (M. van Wyk & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810334.

Basionym: *Ceratocystis tribiliformis* M. van Wyk & M.J. Wingf., Fungal Diversity 21: 197. 2006.

Huntiella tyalla (Kamgan & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810335.
Basionym: *Ceratocystis tyalla* Kamgan & Jol. Roux, Antonie van Leeuwenhoek 101: 233. 2012.

Thielaviopsis Went, Meded. Proefstat. Suikerriet W. Java 5: 4. 1893.

= *Hughesiella* Bat. & A.F. Vital, Anais Soc. Biol. Pernambuco 14: 141. 1956. (type species *Hu. euricoi*).

Type species: *Thielaviopsis ethacetica* Went, Meded. Proefstat. Suikerriet W. Java 5: 4. 1893.

Emended generic diagnosis. *Ascomatal* bases globose, light brown, display dark as result of aleurioconidia and distinctly digitate or stellate appendages. *Ascomatal* necks long, tapering to apex, dark grey. *Ostiole* hyphae divergent, hyaline. *Asci* dehiscent. *Ascospores* aseptate, ellipsoidal, hyaline with sheath. *Conidiophores* lageniform, solitary, occasionally aggregate in synnemata. *Primary conidia* aseptate, cylindrical, hyaline. *Secondary conidia* aseptate, cylindrical to oblong, hyaline becoming grey, thick walled. *Aleurioconidia* subglobose, oblong or ovoid, thick-walled, forms holoblastically, singly or in chains, grey-brown.

Notes: The most distinctive features of this genus are the distinctly digitate or stellate appendages on the ascomatal bases. This is the only group where some species form synnemata in the asexual state. *Thielaviopsis euricoi* is the type species of the genus *Hughesiella*, which is thus a synonym of *Thielaviopsis*.

Thielaviopsis cerberus (Mbenoun, M.J. Wingf. & Jol. Roux) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810336.

Basionym: *Ceratocystis cerberus* Mbenoun, M.J. Wingf. & Jol. Roux, Mycologia 106: 778. 2014.

Thielaviopsis ethacetica Went, Meded. Proefstat. Suikerriet W. Java 5: 4. 1893. (as “*ethaceticus*”).

= *Ceratocystis ethacetica* (Went) Mbenoun & Z.W. de Beer, Mycologia 106: 772. 2014.

= *Endoconidium fragrans* Delacr., Bull. Soc. Mycol. France 9: 184. 1893.

= *Catenularia echinata* Wakker, De ziekten van het suikerriet op Java, E.J. Brill, Leiden: 196. 1898.

Descriptions: Mbenoun *et al.* (2014a).

Note: The synonymy between *T. ethacetica*, *Cat. echinata* and *E. fragrans* is discussed by Mbenoun *et al.* (2014a).

Thielaviopsis euricoi (Bat. & A.F. Vital) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 70. 2002.

Basionym: *Hughesiella euricoi* Bat. & A.F. Vital, Anais Soc. Biol. Pernambuco 14: 142. 1956.

= *Ceratocystis euricoi* (Bat. & A.F. Vital) Mbenoun & Z.W. de Beer, Mycologia 106: 774. 2014.

Descriptions: Mbenoun *et al.* (2014a).

Notes: Sexual state unknown. *Thielaviopsis euricoi* is the type species of the genus *Hughesiella*, treated above as synonym of *Thielaviopsis*.

Thielaviopsis musarum (R.S. Mitchell) Riedl, Sydowia 15: 249. 1962.

Basionym: *Thielaviopsis paradoxa* (De Seynes) Höhn. var. *musarum* R.S. Mitchell, J. Council Sci. Industr. Res. Australia, 10: 130. 1937. (nom. inval., Art. 39.1).

= *Ceratocystis musarum* Riedl, Sydowia 15: 248. 1962.

Descriptions: Mbenoun *et al.* (2014a).

Note: The taxonomy of this species is discussed by Mbenoun *et al.* (2014a).

Thielaviopsis paradoxa (De Seynes) Höhn., Hedwigia 43: 295. 1904.

Basionym: *Sporoschisma paradoxum* De Seynes, Rech. Hist. Nat. Veg. Inf. 3: 30. 1886.

= *Chalara paradoxa* (De Seynes) Sacc., Syll. Fung. 10: 595. 1892.

= *Ceratostomella paradoxa* (De Seynes) Dade, Trans. Br. Mycol. Soc. 13: 191. 1928.

= *Ophiostoma paradoxum* (De Seynes) Nannf., Svenska Skogsv.-Fören. Tidskr. 32: 408. 1934.

= *Endoconidiophora paradoxa* (De Seynes) R.W. Davidson, J. Agric. Res. 50: 802. 1935.

= *Ceratocystis paradoxa* (De Seynes) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.

= *Stilbochalara dimorpha* Ferd. & Winge, Bot. Tidsskr. 30: 220. 1910.

Descriptions: Davidson (1935: 801–802); Hunt (1956: 13, 19–20); Morgan-Jones (1967c, figs A–G); Nag Raj & Kendrick (1975: 112, 114, 128–129, figs 41–42); Upadhyay (1981: 67, figs 197–204); Mbenoun *et al.* (2014a).

Notes: The synonymy of *St. dimorpha* with *C. paradoxa* was suggested by Mbenoun *et al.* (2014a). These authors also discussed and explained the treatment of the names and authorities of the previously considered sexual and asexual states, as suggested by Hawksworth *et al.* (2013).

Thielaviopsis punctulata (Hennebert) A.E. Paulin, T.C. Harr. & McNew, Mycologia 94: 70. 2001.

Basionym: *Chaloropsis punctulata* Hennebert, Antonie van Leeuwenhoek 33: 334. 1967.

- = *Ceratostomella radicolica* Bliss, Mycologia 33: 468. 1941.
 ≡ *Ophiostoma radicololum* (Bliss) Arx, Antonie van Leeuwenhoek 18: 211. 1952.
 ≡ *Ceratocystis radicolica* (Bliss) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.

Descriptions: Hunt (1956: 11, 17, 20); Nag Raj & Kendrick (1975: 106, 142, fig. 38); Upadhyay (1981: 69, figs 205–213); Mbenoun *et al.* (2014a).

Notes: Paulin-Mahady *et al.* (2002) and Mbenoun *et al.* (2014a) confirmed the synonymy of *T. punctulata* and *C. radicolica* based on similar sequences. Based on the Melbourne Code (McNeill *et al.* 2012) the older epithet must take preference, implying that this species will in future be treated as *T. punctulata*, and not as the better known *C. radicolica*, unless conservation of the later name against the earlier is proposed and accepted.

Ceratocystis incertae sedis

Four species could not be consistently accommodated in any of the seven major clades for which genera have been provided. We believe that they represent discrete genera but we have not provided generic names for these lineages. With increased sampling and further study, additional species are likely to be found that will populate these clades. At that time, genera can be provided for them. For the present they have been retained in their existing genera. We also list *C. erinaceus* and *C. norvegica* here for which isolates could not be obtained, and for which the generic placements remains uncertain.

Ceratocystis adiposa (Butler) C. Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 22. 1952.

Basionym: *Sphaeronema adiposum* Butler, Mem. Dept. Agric. India, Bot. Ser. 1: 40. 1906.

- ≡ *Ceratostomella adiposa* (Butler) Sartoris, J. Agric. Res. 35: 585. 1927.
 ≡ *Ophiostoma adiposum* (Butler) Nannf., In Melin & Nannf., Svenska Skogsv.-Fören. Tidskr. 32: 408. 1934.
 ≡ *Endoconidiophora adiposa* (Butler) R.W. Davidson, J. Agric. Res. 50: 802. 1935.
 = *Ceratostomella major* J.F.H. Beyma, Zentrabl. Bakteriol., 2. Abt. 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.

Descriptions: Sartoris (1927: 578–585, figs 1–4); Davidson (1935: 801–802); Hunt (1956: 10–13); Upadhyay (1981: 35, figs 26–30); Moreau (1952: 17–20, fig. 1); Nag Raj & Kendrick (1975: 104, 140, fig. 37).

Notes: Hunt (1956), Moreau (1952), Griffin (1968), Olchowecki & Reid (1974), and Nag Raj & Kendrick (1975), all treated *C. major* and *C. adiposa* as distinct. Upadhyay (1981) suggested the synonymy of *C. major* with *C. adiposa*. Identical SSU sequences for the two species by Hausner *et al.* (1993b) suggested that the synonymy is sound, and this was confirmed in the present study where the two species had identical sequences in ITS, LSU and 60S.

Thielaviopsis basicola (Berk. & Broome) Ferraris, Fl. Ital. Crypt., Fungi 1: 233. 1912.

Basionym: *Torula basicola* Berk. & Broome, Ann. Mag. Nat. Hist. 5: 461. 1850.

- ≡ *Trichocladium basicola* (Berk. & Broome) J.W. Carmich., In: Carmichael *et al.*, Genera of Hyphomycetes: 185. 1980.
 = *Chalara elegans* Nag Raj & W.B. Kendr., Monogr. Chalara: 111. 1975.

Description: Nag Raj & Kendrick (1975: 108–113, figs 39–40 as *Ca. elegans*).

Notes: Sexual state unknown. Delon & Kiffer (1978) synonymised *T. basicola* with *Ca. elegans*, at the time treated in *Chalara* (Nag Raj & Kendrick 1975). Paulin-Mahady *et al.* (2002) showed the species is best treated in *Thielaviopsis*, thus reversing the synonymy and bringing the name to its current state. Although our data have shown that *T. basicola* does not form part of *Thielaviopsis* as defined in the present study, the species is best treated in this genus until an epitype is designated that is linked to the holotype specimen. On that basis a final generic placement can be ascertained.

Ceratocystis erinaceus Bohár, Acta Phytopathol. Entomol. Hung. 31: 215. 1996.

Notes: In the original description of this species from oak in Hungary and the United Kingdom, Bohár (1996) stated that it is closely related, but distinct from *C. virescens* (now *D. virescens*). Apart from a similar host, the elongated, sheathed ascospores of *D. erinaceus* suggest a placement in *Davidsoniella*. However, no cultures were available and we prefer to consider its generic placement as uncertain until epitypification can be achieved.

Ceratocystis fagacearum (Bretz) J. Hunt, Lloydia 19: 21. 1956.

Basionym: *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.

Descriptions: Hunt (1956: 21); Nag Raj & Kendrick (1975: 94, 131, fig. 32A); Upadhyay (1981: 66); Potłajczuk & Schekunova (1985: 150); Kolařík & Hulcr (2009).

Notes: The asexual state of this causal agent of oak wilt was described first as *Ca. quercina* (Henry 1944), while the sexual state was later discovered and described as *E. fagacearum* (Bretz 1952). The isolate used in our study groups outside the major lineages, usually relatively close to, but still very distinct from, *A. ferruginea*. Because this isolate does not represent the type of either of these species, we have chosen to treat the species in *Ceratocystis* until typification can be resolved.

Ambrosiella ferruginea L.R. Batra, Mycologia 59: 980. 1967.

- ≡ *Monilia ferruginea* Math.-Käärik, Meddel. Statens Skogs-Forskningsinst. 43: 57. 1953. (nom. illegit., Art. 53.1, non *M. ferruginea* Pers. 1822).

Descriptions: Mathiesen-Käärik (1953: 53–57, figs 5–7); Batra (1967: 1000–1004, figs 30, 31, 40).

Notes: Sexual state unknown. In our analyses, this species did not group in *Ambrosiella s. str.*, but relatively close to, but still very distinct from, *C. fagacearum*. Because the isolate used in

our study does not represent the type for the species, it is best treated in *Ambrosiella* until typification can be achieved.

Ceratocystis norvegica J. Reid & Hausner, Botany 88: 977. 2010.

Notes: A culture for this species could not be obtained. The sequences generated by Reid *et al.* (2010) suggest that this species falls outside the *C. coerulescens* complex (now *Endoconidiophora*), in which it would otherwise fit based on morphology and its conifer host. An accurate generic placement will only be possible once a culture can be obtained from which the appropriate sequences can be generated. Until such time it is best treated in *Ceratocystis s.l.*

DISCUSSION

Ceratocystis s. str. as it is defined in the present study is typified by the well-known species *C. fimbriata*. The genus currently includes 32 species, all of which were included in the analyses making up this study. The genus includes many important plant pathogens of angiosperm trees, but also of root crops (Kile 1993, Engelbrecht & Harrington 2005, Van Wyk *et al.* 2013, Roux & Wingfield 2013). These fungi all have ascomata with smooth non-ornamented bases and hat-shaped ascospores; two morphological features that distinguish them from species now in the genera *Thielaviopsis* (previously *C. paradoxa s.l.*) and *Huntia* (previously *C. moniliformis s.l.*). Both the latter genera have ornamented ascomatal bases, although the morphology of the ornamentations is different in the two genera.

In some cases, species boundaries for *Ceratocystis s. str.* are very clear, for example in the cases of the tree pathogens *C. platani*, *C. cacaofunesta*, and *C. albifundus* (Wingfield *et al.* 1996, Engelbrecht & Harrington 2005). In others, distinction at the species level has been debated (Fourie *et al.* 2014, Harrington *et al.* 2014a). Problems have for example arisen where the ITS region has suggested the existence of species boundaries but where it is now recognised that there are often two or more ITS forms within a single isolate (Al Adawi *et al.* 2013, Naidoo *et al.* 2013, Harrington *et al.* 2014a). Revisions of these species boundaries are likely to emerge when additional tools, especially those taken from whole genome sequences (Wilken *et al.* 2013), become available to discriminate more clearly between species. Another problem, already recognised for this group, is that hybridisation has occurred between species (Engelbrecht & Harrington 2005), a factor that will also confuse the recognition of discrete taxa. What is clear, however, is that there are many species already known in this group and many more will likely be found in the future.

The asexual genus *Chalaropsis* has been emended to accommodate three species that are found on woody substrates. Two of these three were included in the analyses, along with information from a fourth undescribed species discovered in a culture collection. None of these fungi are known to have any economic or critical important ecological significance.

The genus *Endoconidiophora* was emended to accommodate an important group of eight species that occur mostly on conifers and many of which are symbionts of conifer-infesting bark beetles. These fungi have previously been referred to as “the Gymnosperm section” in the *C. coerulescens s.l.* group

(Harrington 2009, Wingfield *et al.* 2013) and they include a number of important pathogenic species such as *E. polonica*, *E. laricicola*, *E. laricis* and *E. rufipennis* (Redfern *et al.* 1987, Christiansen & Solheim 1990, Solheim & Safranyik 1997, Yamaoka *et al.* 1998). Other species are mostly agents of sap stain in conifer timber. Unlike species in *Ceratocystis s. s.*, *Huntia* and *Thielaviopsis* as circumscribed here, these fungi have ascospores that are not hat-shaped but rather are obovoid, with distinct sheaths (Fig. 3). *Ceratocystis norvegica*, a species from conifers in Norway (Reid *et al.* 2010) that seems to fit the description of *Endoconidiophora*, but for which material was not available, should be considered in future treatments of this genus.

Davidsoniella is described as a new genus to accommodate members of what has previously been referred to as “the Angiosperm section” of *C. coerulescens s.l.* (Harrington 2009, Wingfield *et al.* 2013). The group includes four species, of which two, *D. virescens* and *D. eucalypti*, have known sexual states. The fusiform ascospores with evenly distributed hyaline sheaths are similar to but distinct from those of species now accommodated in *Endoconidiophora*. The remaining two species (*D. australis* and *D. neocaledoniae*) are known only by their asexual morphs, with the “chalara- or thielaviopsis-like” morphology typical of all species in *Ceratocystis s.l.* other than *Ambrosiella*. Interestingly, three of these fungi (*D. virescens*, *D. neocaledoniae* and *D. australis*) are important tree pathogens (Hepting 1944, Dadant 1950, Kile & Walker 1987) while one (*D. eucalypti*) is not known to be a pathogen (Kile *et al.* 1996). Three species (*D. eucalypti*, *D. neocaledoniae* and *D. australis*) are known exclusively from Australasia, while *D. virescens* occurs in North America. One more species fits the description of *Davidsoniella*, namely *C. erinaceus* from oak in Europe (Bohár 1996). No sequence data exist for this species but it should be considered in future treatments of this genus.

The emended asexual genus *Thielaviopsis* includes species previously placed in *C. paradoxa s.l.*, some of which have known sexual states. Until recently all species in this group were aggregated in the single species, *C. paradoxa*, but Mbenoun *et al.* (2014b)'s sequencing and mating studies disclosed six species in what they referred to as the *C. paradoxa* complex. They showed that the type species of *Thielaviopsis*, *T. ethacetica*, though previously treated as anamorph of *C. paradoxa* (Nag Raj & Kendrick 1975), is a distinct species. In one species, *T. euricoi*, no sexual state has been observed, but the others all produce hat-shaped ascospores. The outstanding characteristic of this genus, however, is the presence of prominent, digitate appendages on the ascomatal bases (Fig. 2). Most of these fungi occur on monocotyledonous plants including palms, pineapple and banana and some are important plant pathogens (Mitchell 1937, Bliss 1941, Abdullah *et al.* 2009).

Huntia was established in this study to accommodate a well-recognised and large group of species that have previously been referred to as residing in *C. moniliformis s.l.* Nineteen species are recognised in *Huntia* of which 18 were included in the analyses. Two of these species are in the process of being described (Mbenoun unpubl. data). Species of *Huntia* have hat-shaped ascospore (Fig. 3) similar to those found in *Ceratocystis s. str.* but they have very distinct ascomata. The latter feature necks with basal plates that easily disconnect from the ascomatal bases, which are also ornamented with spines (Fig. 2). *Huntia* spp. are very commonly encountered on tree

wounds and they are typically non-pathogenic (Roux *et al.* 2004, Tarigan *et al.* 2010, Van Wyk *et al.* 2011).

The genus *Ambrosiella* is perhaps the most unusual in *Ceratocystis s. l.* The five species accommodated in this genus (three of which were included in the analyses) are all symbionts of wood-boring “ambrosia” beetles and they lack a known sexual state. They are the only species in *Ceratocystis s. l.* that do not have typical “chalara-like” conidiogenous cells. Instead they have tubular tapering conidiophores and rectangular conidia formed in chains.

Four species in *Ceratocystis s. l.* did not reside in any of the six major phylogenetic clades arising from this study. These species included *C. adiposa*, *C. fagacearum*, *Thielaviopsis basicola* and *Ambrosiella ferruginea*. These clearly represent discrete genera, which as collections increase in the future, will most likely accommodate additional species. This would be the same situation that has arisen for other genera now recognised in *Ceratocystis s. l.* and that previously included very few obvious species. For the present, we have chosen not to provide generic descriptions for these species. We believe that they are likely to be more clearly defined in the future, particularly since three of the four require additional work to obtain living material that can be unambiguously reconciled with their typification. Three of these four fungi (*C. fagacearum*, *C. adiposa* and *T. basicola*) are well-recognised plant pathogens (Butler 1906, Yarwood 1981, Juzwik *et al.* 2008) and we recognise that name changes could cause some confusion. It will thus be important to make it clear in studies that these fungi are phylogenetically unrelated to the genera in which they are currently treated.

Phylogenetic analyses based on three carefully selected gene regions in this study have provided robust data to be able to distinguish more effectively between a large number of important and very different fungi that have, for many years, been unfortunately lumped in a single genus. The improved resolution has emerged through intensive collecting initiatives in new areas and through the application of new technologies that have improved our ability to recognise cryptic taxa. As global collecting initiatives expand for fungi residing in the *Ceratocystidaceae*, the taxa accommodated in the genera established in this study will surely increase and the boundaries of the few remaining monotypic lineages will also be elucidated.

The new and rapidly stabilising nomenclatural code for fungi (McNeill *et al.* 2012) underpins a natural classification and a single name for all fungal taxa. This is a major and positive change that will ultimately promote a more effective taxonomy for fungi and it will ensure easier relationships with important associated disciplines such as plant pathology (Hawksworth 2011, Wingfield *et al.* 2012). A one fungus one name scheme has already been presented for the so-called ophiostomatoid fungi including the *Ceratocystidaceae* (De Beer *et al.* 2013b). In the present study, we have followed this approach rigorously. As far as possible, available generic names, in all cases those associated with asexual morphs have been used. In two instances entirely new generic names have been established and these honour two important early pioneers of the taxonomy of the ophiostomatoid fungi. They are John Hunt who produced the first comprehensive monograph of *Ceratocystis* (Hunt 1956) and Ross W. Davidson who dedicated his career to collecting, identifying and describing species of ophiostomatoid fungi including several *Ceratocystis* spp.

ACKNOWLEDGEMENTS

For invaluable assistance in various aspects of this work, we thank Rouxle Botha, Arista Fourie, Seonju Marinowitz, Michael Mbenoun, Kershnee Naidoo and Markus Wilken. Photos were kindly made available by Ali Al-Adawi, Ronald Heath, Thomas Kirisits, DongHyeon Lee, Michael Mbenoun, Jolanda Roux, Marthin Tarigan and Gilbert Kamgan Nkuekam. We are thankful to Benjamin Stielow and the Barcoding Consortium for allowing us access to unpublished primers to use in this paper. We also acknowledge the financial support of members of the Tree Protection Cooperative Programme (TCP), the NRF/DST Centre of Excellence in Tree Health Biotechnology (CTHB), and the University of Pretoria.

REFERENCES

- Abdullah S, Asensio L, Monfort E, *et al.* (2009). Incidence of the two date palm pathogens, *Thielaviopsis paradoxa* and *T. punctulata* in soil from date palm plantations in Elx, South-East Spain. *Journal of Plant Protection Research* **49**: 276–279.
- Al Adawi AO, Barnes I, Khan IA, *et al.* (2013). *Ceratocystis manginecans* associated with a serious wilt disease of two native legume trees in Oman and Pakistan. *Australasian Plant Pathology* **42**: 179–193.
- Alvarez E, Llano GA, Loke JB, *et al.* (2012). Characterization of *Thielaviopsis paradoxa* Isolates from Oil Palms in Colombia, Ecuador and Brazil. *Journal of Phytopathology* **160**: 690–700.
- Baker Engelbrecht CJ, Harrington TC, Krauss U, *et al.* (2003). Genetic variability and host specialization in the Latin American clade of *Ceratocystis fimbriata*. *Phytopathology* **93**: 1274–1284.
- Bakshi BK (1951). Studies on four species of *Ceratocystis*, with a discussion on fungi causing sap-stain in Britain. *Mycological Papers* **35**: 1–16.
- Barnes I, Gaur A, Burgess T, *et al.* (2001). Microsatellite markers reflect intra-specific relationships between isolates of the vascular wilt pathogen. *Ceratocystis fimbriata*. *Molecular Plant Pathology* **2**: 319–325.
- Barnes I, Roux J, Wingfield BD, *et al.* (2003). *Ceratocystis pirilliformis*, a new species from *Eucalyptus nitens* in Australia. *Mycologia* **95**: 865–871.
- Batista AC, Vital AF (1956). *Hughesiella* – novo e curioso genero de fungos Dematiaceae. *Anais da Sociedade de Biologia de Pernambuco* **14**: 141–144.
- Batra LR (1967). Ambrosia fungi: A taxonomic revision, and nutritional studies of some species. *Mycologia* **59**: 976–1017.
- Bliss DE (1941). A new species of *Ceratostomella* on the date palm. *Mycologia* **33**: 468–482.
- Bohár G (1996). *Ceratocystis erinaceus*: A new endophyte in the heartwood of oak. *Acta Phytopathologica et Entomologica Hungarica* **31**: 213–218.
- Brader L (1964). Étude de la relation entre le scolyte des rameaux du Caféier, *Xyleborus compactus* Eichh. (*X. morstatti* Hag.) et sa plante-hôte. *Mededelingen van de Landbouwhogeschool, Wageningen, Nederland* **64**: 1–109.
- Bretz TW (1952). The ascigerous stage of the Oak wilt fungus. *Phytopathology* **42**: 435–437.
- Butler EJ (1906). Fungus diseases of sugar-cane in Bengal. *Memoirs of the Department of Agriculture in India. Botanical Series* **1**: 1–53.
- Christiansen E, Solheim H (1990). The bark beetle-associated blue-stain fungus *Ophiostoma polonicum* can kill various spruces and Douglas-fir. *European Journal of Forest Pathology* **20**: 436–446.
- Dadant R (1950). Sur une nouvelle maladie du *Coffea robusta* en Nouvelle Calédonie. *Revue Générale de Botanique* **57**: 1–11.
- Davidson RW (1935). Fungi causing stain in logs and lumber in the Southern States, including five new species. *Journal of Agricultural Research* **50**: 789–807.
- De Beer ZW, Seifert KA, Wingfield MJ (2013a). The ophiostomatoid fungi: their dual position in the Sordariomycetes. In: *The ophiostomatoid fungi: expanding frontiers* (Seifert KA, De Beer ZW, Wingfield MJ, eds), *CBS biodiversity series*, vol. **12**. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 1–19.
- De Beer ZW, Seifert KA, Wingfield MJ (2013b). A nomenclator for ophiostomatoid genera and species in the *Ophiostomatales* and *Microascales*. In: *The ophiostomatoid fungi: expanding frontiers* (Seifert KA, De Beer ZW, Wingfield MJ, eds), *CBS biodiversity series*, vol. **12**. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 245–322.
- Delon R, Kiffer E (1978). *Chalara elegans* (*Thielaviopsis basicola*) et les especes voisines. 1-Generalites et pathologie. *Annales du Tabac* **2**: 159–186.

- Duong TA, De Beer ZW, Wingfield BD, *et al.* (2012). Phylogeny and taxonomy of species in the *Grosmannia serpens* complex. *Mycologia* **104**: 715–732.
- Engelbrecht CJB, Harrington TC (2005). Intersterility, morphology and taxonomy of *Ceratocystis fimbriata* on sweet potato, cacao and sycamore. *Mycologia* **97**: 57–69.
- Engelbrecht CJ, Harrington TC, Alfenas A (2007). *Ceratocystis* wilt of cacao — a disease of increasing importance. *Phytopathology* **97**: 1648–1649.
- Engelbrecht CJB, Harrington TC, Steimel J, *et al.* (2004). Genetic variation in eastern North American and putatively introduced populations of *Ceratocystis fimbriata* f. *platani*. *Molecular Ecology* **13**: 2995–3005.
- Fourie A, Wingfield MJ, Wingfield BD, *et al.* (2014). Molecular markers delimit cryptic species in the *Ceratocystis fimbriata sensu lato* complex. *Mycological Progress*: (in press).
- Gibbs JN (1981). European forestry and *Ceratocystis* species. *EPPO Bulletin* **11**: 193–197.
- Gibbs JN (1993). The biology of ophiostomatoid fungi causing sapstain in trees and freshly cut logs. In: *Ceratocystis and ophiostoma: taxonomy, ecology and pathogenicity* (Wingfield MJ, Seifert KA, Webber J, eds). APS Press, St. Paul, Minnesota: 153–160.
- Griffin HD (1968). The genus *Ceratocystis* in Ontario. *Canadian Journal of Botany* **46**: 689–718.
- Halsted BD (1890). Some fungous diseases of the sweet potato. *Bulletin of the New Jersey Agricultural Experiment Station* **76**: 3–32.
- Harrington TC (1988). *Leptographium* species, their distributions, hosts and insect vectors. In: *Leptographium root diseases on conifers* (Harrington TC, Cobb FW, eds). APS Press, St. Paul, Minnesota: 1–40.
- Harrington TC (2000). Host specialization and speciation in the American wilt pathogen *Ceratocystis fimbriata*. *Fitopatologia Brasileira* **25**: 262–263.
- Harrington TC (2009). The genus *Ceratocystis*. Where does the oak wilt fungus fit? In: *Proceedings of the 2nd National Oak Wilt Symposium* (Appel DN, Billings RF, eds). USDA Forest Service, Forest Health Protection, Austin, Texas: 1–16.
- Harrington TC, Aghayeva DN, Fraedrich SW (2010). New combinations in *Raffaella*, *Ambrosiella*, and *Hyalorhinochlaidiella*, and four new species from the redbay ambrosia beetle, *Xyleborus glabratus*. *Mycotaxon* **111**: 337–361.
- Harrington TC, Kazmi MR, Al-Sadi AM, *et al.* (2014a). Intraspecific and intragenomic variability of ITS rDNA sequences reveals taxonomic problems in *Ceratocystis fimbriata sensu stricto*. *Mycologia* **106**: 224–242.
- Harrington TC, McNew D, Mayers C, *et al.* (2014b). *Ambrosiella roeperi* sp. nov. is the mycangial symbiont of the granulate ambrosia beetle, *Xylosandrus crassiusculus*. *Mycologia* **106**: 835–845.
- Harrington TC, Pashenova NV, McNew DL, *et al.* (2002). Species delimitation and host specialization of *Ceratocystis laricicola* and *C. polonica* to larch and spruce. *Plant Disease* **86**: 418–422.
- Harrington TC, Wingfield MJ (1998). The *Ceratocystis* species on conifers. *Canadian Journal of Botany* **76**: 1446–1457.
- Hausner G, Reid J, Klassen GR (1993a). On the phylogeny of *Ophiostoma*, *Ceratocystis* s.s., and *Microascus*, and relationships within *Ophiostoma* based on partial ribosomal DNA sequences. *Canadian Journal of Botany* **71**: 1249–1265.
- Hausner G, Reid J, Klassen GR (1993b). On the subdivision of *Ceratocystis* s.l., based on partial ribosomal DNA sequences. *Canadian Journal of Botany* **71**: 52–63.
- Hawksworth DL (2011). A new dawn for the naming of fungi: impacts of decisions made in Melbourne in July 2011 on the future publication and regulation of fungal names. *Mycologia* **1**: 7–20.
- Hawksworth DL, Crous PW, Redhead SA, *et al.* (2011). The Amsterdam declaration on fungal nomenclature. *IMA Fungus* **2**: 105–112.
- Hawksworth DL, McNeill J, De Beer ZW, *et al.* (2013). Names of fungal species with the same epithet applied to different morphs: how to treat them. *IMA Fungus* **4**: 53–56.
- Hedgcock GG (1906). Studies upon some chromogenic fungi which discolor wood. *Missouri Botanical Garden Annual Report* **17**: 59–114.
- Henry BW (1944). *Chalara quercina* n. sp., the cause of Oak wilt. *Phytopathology* **34**: 631–635.
- Hepting G (1944). Sapstreak, a new killing disease of sugar maple. *Phytopathology* **34**: 1069–1076.
- Hibbett DS, Binder M, Bischoff JF, *et al.* (2007). A higher-level phylogenetic classification of the Fungi. *Mycological Research* **111**: 509–547.
- Hunt J (1956). Taxonomy of the genus *Ceratocystis*. *Lloydia* **19**: 1–58.
- Johnson JA, Harrington TC, Engelbrecht CJB (2005). Phylogeny and taxonomy of the North American clade of the *Ceratocystis fimbriata* complex. *Mycologia* **97**: 1067–1092.
- Juzwik J, Harrington TC, MacDonald WL, *et al.* (2008). The origin of *Ceratocystis fagacearum*, the oak wilt fungus. *Annual Review of Phytopathology* **46**: 13–26.
- Kamgan Nkuekam G, Wingfield MJ, Mohammed C, *et al.* (2012). *Ceratocystis* species, including two new species associated with nitidulid beetles, on eucalypts in Australia. *Antonie Van Leeuwenhoek* **101**: 217–241.
- Katoh K, Standley DM (2013). MAFFT Multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780.
- Kiffer E, Delon R (1983). *Chalara elegans* (*Thielaviopsis basicola*) and allied species. II — validation of two taxa. *Mycotaxon* **18**: 165–174.
- Kile GA (1993). Plant diseases caused by species of *Ceratocystis sensu stricto* and *Chalara*. In: *Ceratocystis and ophiostoma: taxonomy, ecology and pathogenicity* (Wingfield MJ, Seifert KA, Webber J, eds). APS Press, St. Paul, Minnesota: 173–183.
- Kile GA, Harrington TC, Yuan ZQ, *et al.* (1996). *Ceratocystis eucalypti* sp. nov., a vascular stain fungus from eucalypts in Australia. *Mycological Research* **100**: 571–579.
- Kile G, Walker J (1987). *Chalara australis* sp. nov. (Hyphomycetes), a vascular pathogen of *Nothofagus cunninghamii* (Fagaceae) in Australia and its relationship to other *Chalara* species. *Australian Journal of Botany* **35**: 1–32.
- Kirisits T, Konrad H, Wingfield MJ, Chhetri DB (2013). Ophiostomatoid fungi associated with the Eastern Himalayan spruce bark beetle, *Ips schmutzenhoferi*, in Bhutan and their pathogenicity to *Picea spinulosa* and *Pinus wallichiana*. In: *The ophiostomatoid fungi: expanding frontiers* (Seifert KA, De Beer ZW, Wingfield MJ, eds), *CBS biodiversity series*, vol. **12**. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 99–112.
- Kolarik M, Hulcr J (2009). Mycobiota associated with the ambrosia beetle *Scolytodes unipunctatus* (Coleoptera: Curculionidae, Scolytinae). *Mycological Research* **113**: 44–60.
- Kowalski T, Butin H (1989). Taxonomie bekannter und neuer *Ceratocystis*-Arten an Eiche (*Quercus robur* L.). *Journal of Phytopathology* **124**: 236–248.
- Lagerberg T, Lundberg G, Melin E (1927). Biological and practical researches into blueing in pine and spruce. *Svenska Skogsvårdsföreningens Tidskrift* **25**: 145–272.
- Luc M (1952). *Ophiostoma moniliforme* (Hedge.) H. et P. Syd. et ses diverses formes. *Revue de Mycologie* **17**: 10–16.
- Lutzoni F, Kauff F, Cox CJ, *et al.* (2004). Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. *American Journal of Botany* **91**: 1446–1480.
- Maekawa N, Tsuneda A, Arita I (1987). *Ceratocystis* species occurring on the *Lentinus edodes* bedlogs. *Reports of the Tottori Mycological Institute* **25**: 6–14.
- Malloch DW, Blackwell M (1993). Dispersal biology of the ophiostomatoid fungi. In: *Ceratocystis and ophiostoma: taxonomy, ecology and pathogenicity* (Wingfield MJ, Seifert KA, Webber J, eds). APS Press, St. Paul, Minnesota: 195–206.
- Marin M, Castro B, Gaitan A, *et al.* (2003). Relationships of *Ceratocystis fimbriata* isolates from Colombian coffee-growing regions based on molecular data and pathogenicity. *Journal of Phytopathology* **151**: 395–405.
- Marin M, Preisig O, Wingfield BD, *et al.* (2005). Phenotypic and DNA sequence data comparisons reveal three discrete species in the *Ceratocystis polonica* species complex. *Mycological Research* **109**: 1137–1148.
- Marin M, Preisig O, Wingfield BD, *et al.* (2009). Single sequence repeat markers reflect diversity and geographic barriers in Eurasian populations of the conifer pathogen *Ceratocystis polonica*. *Forest Pathology* **39**: 249–265.
- Mathiesen A (1951). Einige neue *Ophiostoma*-Arten in Schweden. *Svensk Botanisk Tidskrift* **45**: 203–232.
- Mathiesen-Käärik A (1953). Eine Übersicht über die gewöhnlichsten mit Borkenkäfern assoziierten Bläuepilze in Schweden und einige für Schweden neue Bläuepilze. *Meddelanden från Statens Skogsforskningsinstitut* **43**: 1–74.
- Matsushima T (1975). *Icones microfungorum a Matsushima lectorum*. Matsushima, Kobe, Japan.
- Mbenoun M, De Beer ZW, Wingfield MJ, *et al.* (2014a). Reconsidering species boundaries in the *Ceratocystis paradoxa* complex, including a new species from oil palm and cacao in Cameroon. *Mycologia* **106**: 757–784.
- Mbenoun M, Wingfield M, Begoude Boyogueno A, *et al.* (2014b). Molecular phylogenetic analyses reveal three new *Ceratocystis* species and provide evidence for geographic differentiation of the genus in Africa. *Mycological Progress* **13**: 219–240.
- McNeill J, Barrie FR, Buck WR, *et al.* (2012). Regnum Vegetabile. *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code)*: vol. **154**. Koeltz Scientific Books, Germany.

- Melin E, Nannfeldt JA (1934). Researches into the blueing of ground wood-pulp. *Svenska Skogsvårdsföreningens Tidskrift* **32**: 397–616.
- Mitchell RS (1937). Stem end rot of bananas with special reference to the physiological relationships of *Thielaviopsis paradoxa* (De Seyes) von Höhn. *Journal of the Council for Scientific and Industrial Research Australia* **10**: 123–130.
- Moreau C (1952). Coexistence des formes *Thielaviopsis* et *Graphium* chez une souche de *Ceratocystis major* (van Beyma) nov. comb. Remarques sur les variations des *Ceratocystis*. *Revue de Mycologie (Suppl. Colonial)* **17**: 17–25.
- Moreau F, Moreau M (1952). Sur le développement du *Ceratocystis moniliformis* (Hedgcock) nov. comb. *Revue de Mycologie* **17**: 141–153.
- Morgan-Jones G (1967a). *Ceratocystis fimbriata*. *IMI Descriptions of Fungi and Bacteria* **15**. Sheet 141.
- Morgan-Jones G (1967b). *Ceratocystis moniliformis*. *IMI Descriptions of Fungi and Bacteria* **15**. Sheet 142.
- Morgan-Jones G (1967c). *Ceratocystis paradoxa*. *IMI Descriptions of Fungi and Bacteria* **15**. Sheet 143.
- Münch E (1907). Die Blaufäule des Nadelhozes. I-II. *Naturwissenschaftliche Zeitschrift für Forst- und Landwirtschaft* **5**: 531–573.
- Nag Raj TR, Kendrick B (1975). *A monograph of Chalara and allied genera*. Wilfrid Laurier University Press, Waterloo, Canada.
- Naidoo K, Steenkamp ET, Coetzee MPA, et al. (2013). Concerted evolution in the ribosomal RNA cistron. *PLoS One* **8**: e59355.
- Norvell LL (2011). Fungal nomenclature. 1. Melbourne approves a new Code. *Mycotaxon* **116**: 481–490.
- Ocasio-Morales RG, Tsopelas P, Harrington TC (2007). Origin of *Ceratocystis platani* on native *Platanus orientalis* in Greece and its impact on natural forests. *Plant Disease* **91**: 901–904.
- Olchowecki A, Reid J (1974). Taxonomy of the genus *Ceratocystis* in Manitoba. *Canadian Journal of Botany* **52**: 1675–1711.
- Paulin-Mahady AE, Harrington TC, McNew D (2002). Phylogenetic and taxonomic evaluation of *Chalara*, *Chalaropsis*, and *Thielaviopsis* anamorphs associated with *Ceratocystis*. *Mycologia* **94**: 62–72.
- Peyronel B (1916). Una nuova malattia del lupino prodotta da *Chalaropsis thielavioides* Peyr. *Le Stazioni Sperimentali Agrarie Italiane* **49**: 583–596.
- Pontis RE (1951). A canker disease of the coffee tree in Colombia and Venezuela. *Phytopathology* **41**: 178–184.
- Potlajczuk VI, Schekunova EG (1985). De distributione specierum generic *Ceratocystis* Ell. et Halst. emend. Bakshi in URSS. *Novosti Sistematiki nizsich rastleniy "Nauka" Akademia Nauk SSSR* **22**: 148–156.
- Réblová M, Gams W, Seifert KA (2011). *Monilochaetes* and allied genera of the *Glomerellales*, and a reconsideration of families in the *Microascales*. *Studies in Mycology* **68**: 163–191.
- Redfern DB, Stoakley JT, Steele H, et al. (1987). Dieback and death of larch caused by *Ceratocystis laricicola* sp. nov. following attack by *Ips cembrae*. *Plant Pathology* **36**: 467–480.
- Reid J, Iranpour M, Rudski SM, et al. (2010). A new conifer-inhabiting species of *Ceratocystis* from Norway. *Botany* **88**: 971–983.
- Ronquist F, Teslenko M, van der Mark P, et al. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539–542.
- Roux J, Van Wyk M, Hatting H, et al. (2004). *Ceratocystis* species infecting stem wounds on *Eucalyptus grandis* in South Africa. *Plant Pathology* **53**: 414–421.
- Roux J, Wingfield MJ (2013). *Ceratocystis* species on the African continent, with particular reference to *C. albifundus*, and African species in the *C. fimbriata sensu lato* species complex. In: *The ophiostomatoid fungi: expanding frontiers* (Seifert KA, De Beer ZW, Wingfield MJ, eds), *CBS biodiversity series*, vol. **12**. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 131–138.
- Samuels GJ (1993). The case for distinguishing *Ceratocystis* and *Ophiostoma*. In: *Ceratocystis and ophiostoma: taxonomy, ecology and pathogenicity* (Wingfield MJ, Seifert KA, Webber J, eds). APS Press, St. Paul, Minnesota: 15–20.
- Santini A, Capretti P (2000). Analysis of the Italian population of *Ceratocystis fimbriata* f.sp. *platani* using RAPD and minisatellite markers. *Plant Pathology* **49**: 461–467.
- Sartoris GB (1927). A cytological study of *Ceratostomella adiposum* (Butl.) comb. nov., the black-rot fungus of sugar-cane. *Journal of Agricultural Research* **35**: 577–583.
- Schoch CL, Seifert KA, Huhndorf S, et al. (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proceedings of the National Academy of Sciences of the United States of America* **109**: 6241–6246.
- Seifert KA (1993). Sapstain of commercial lumber by species of *Ophiostoma* and *Ceratocystis*. In: *Ceratocystis and ophiostoma: taxonomy, ecology and pathogenicity* (Wingfield MJ, Seifert KA, Webber J, eds). APS Press, St. Paul, Minnesota: 141–151.
- Seifert KA, De Beer ZW, Wingfield MJ (2013). *The ophiostomatoid fungi: expanding frontiers*. *CBS biodiversity series*: vol. **12**. CBS-KNAW Biodiversity Centre, Utrecht, The Netherlands.
- Seifert KA, Morgan-Jones G, Gams W, et al. (2011). *The genera of hyphomycetes*. *CBS biodiversity series*: vol. **9**. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands.
- Seifert KA, Wingfield MJ, Kendrick WB (1993). A nomenclator for described species of *Ceratocystis*, *Ophiostoma*, *Ceratocystiopsis*, *Ceratostomella* and *Sphaeronaemella*. In: *Ceratocystis and ophiostoma: taxonomy, ecology and pathogenicity* (Wingfield MJ, Seifert KA, Webber J, eds). APS Press, St. Paul, Minnesota: 269–287.
- Siemaszko W (1939). Zespoly grzybów towarzyszących kornikom polskim. *Planta Polonica* **7**: 1–54.
- Silvestro D, Michalak I (2012). raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity & Evolution* **12**: 335–337.
- Solheim H (1986). Species of *Ophiostomataceae* isolated from *Picea abies* infested by the bark beetle *Ips typographus*. *Nordic Journal of Botany* **6**: 199–207.
- Solheim H, Safranyik L (1997). Pathogenicity to Sitka spruce of *Ceratocystis rufipenni* and *Leptographium abietinum*, blue-stain fungi associated with the spruce beetle. *Canadian Journal of Forest Research* **27**: 1336–1341.
- Stielow JB, Vries de M, Dukik K, et al. (2014). One fungus, which genes? Benchmarking primers for potential secondary DNA barcodes. *Persoonia* **33**: (in press).
- Spatafora JW, Blackwell M (1994). The polyphyletic origins of ophiostomatoid fungi. *Mycological Research* **98**: 1–9.
- Steimel J, Engelbrecht CJB, Harrington TC (2004). Development and characterization of microsatellite markers for the fungus *Ceratocystis fimbriata*. *Molecular Ecology Notes* **4**: 215–218.
- Sydow vH, Sydow P (1919). Mycologische Mitteilungen. *Annales Mycologici* **17**: 33–47.
- Tamura K, Stecher G, Peterson D, et al. (2013). MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* **30**: 2725–2729.
- Tarigan M, Roux J, Van Wyk M, et al. (2011). A new wilt and die-back disease of *Acacia mangium* associated with *Ceratocystis manginecans* and *C. acaciivora* sp. nov. in Indonesia. *South African Journal of Botany* **77**: 292–304.
- Tarigan M, Van Wyk M, Roux J, et al. (2010). Three new *Ceratocystis* spp. in the *Ceratocystis moniliformis* complex from wounds on *Acacia mangium* and *A. crassicarpa*. *Mycoscience* **51**: 53–67.
- Thorpe DJ, Harrington TC, Uchida JY (2005). Pathogenicity, internal transcribed spacer-rDNA variation, and human dispersal of *Ceratocystis fimbriata* on the family *Araceae*. *Phytopathology* **95**: 316–323.
- Upadhyay HP (1981). *A monograph of Ceratocystis and Ceratocystiopsis*. University of Georgia Press, Athens, GA, USA.
- Van der Nest MA, Bihon W, De Vos L, et al. (2014). Draft genome sequences of *Diplodia sapinea*, *Ceratocystis manginecans*, and *Ceratocystis moniliformis*. *IMA Fungus* **5**: 135–140.
- Van Wyk M, Al Adawi AO, Khan IA, et al. (2007). *Ceratocystis manginecans* sp. nov., causal agent of a destructive mango wilt disease in Oman and Pakistan. *Fungal Diversity* **27**: 213–230.
- Van Wyk M, Wingfield BD, Marin M, et al. (2010). New *Ceratocystis* species infecting coffee, cacao, citrus and native trees in Colombia. *Fungal Diversity* **40**: 103–117.
- Van Wyk M, Wingfield BD, Wingfield MJ (2011). Four new *Ceratocystis* spp. associated with wounds on *Eucalyptus*, *Schizolobium* and *Terminalia* trees in Ecuador. *Fungal Diversity* **46**: 111–131.
- Van Wyk M, Wingfield BD, Wingfield MJ (2013). *Ceratocystis* species in the *Ceratocystis fimbriata* complex. In: *The ophiostomatoid fungi: expanding frontiers* (Seifert KA, De Beer ZW, Wingfield MJ, eds), *CBS biodiversity series*, vol. **12**. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 65–73.
- Van Wyk PWJ, Wingfield MJ, Van Wyk PS (1993). Ultrastructure of centrum and ascospore development in selected *Ceratocystis* and *Ophiostoma* species. In: *Ceratocystis and ophiostoma: taxonomy, ecology and pathogenicity* (Wingfield MJ, Seifert KA, Webber J, eds). APS Press, St. Paul, Minnesota: 195–206.

- Veldeman R (1971). '*Chalaropsis* sp.' a new parasitic fungus on poplar, the cause of bark lesions. *Mededelingen van de Facultiet Landbouwwetenschappen, Rijksuniversiteit Gent* **36**: 1001–1005.
- Vilgalys R, Hester M (1990). Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172**: 4238–4246.
- Visser C, Wingfield MJ, Wingfield BD, *et al.* (1995). *Ophiostoma polonicum* is a species of *Ceratocystis sensu stricto*. *Systematic and Applied Microbiology* **18**: 403–409.
- Von Arx JA, Hennebert GL (1965). Deux champignons ambrosia. *Mycopathologia et Mycologia Applicata* **25**: 309–315.
- Webster RK, Butler EE (1967). A morphological and biological concept of the species *Ceratocystis fimbriata*. *Canadian Journal of Botany* **45**: 1457–1468.
- Went FAFC (1893). De ananasziekte van het suikerriet. *Mededeelingen van het Proefstation West-Java* **5**: 1–8.
- Wilken PM, Steenkamp ET, Wingfield MJ, *et al.* (2013). Draft nuclear genome sequence for the plant pathogen, *Ceratocystis fimbriata*. *IMA Fungus* **4**: 357–358.
- Wingfield BD, Van Wyk M, Roos H, *et al.* (2013). *Ceratocystis*: emerging evidence for discrete generic boundaries. In: *The ophiostomatoid fungi: expanding frontiers* (Seifert KA, De Beer ZW, Wingfield MJ, eds), CBS biodiversity series, vol. 12. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands: 57–64.
- Wingfield MJ, De Beer C, Visser C, *et al.* (1996). A new *Ceratocystis* species defined using morphological and ribosomal DNA sequence comparisons. *Systematic and Applied Microbiology* **19**: 191–202.
- Wingfield MJ, De Beer ZW, Slippers B, *et al.* (2012). One fungus, one name promotes progressive plant pathology. *Molecular Plant Pathology* **13**: 604–613.
- Wingfield MJ, Harrington TC, Solheim H (1997). Two species in the *Ceratocystis coerulescens* complex from conifers in western North America. *Canadian Journal of Botany* **75**: 827–834.
- Witthuhn RC, Harrington TC, Steimel JP, *et al.* (2000). Comparison of isozymes, rDNA spacer regions and MAT-2 DNA sequences as phylogenetic characters in the analysis of the *Ceratocystis coerulescens* complex. *Mycologia* **92**: 447–452.
- Witthuhn RC, Wingfield BD, Wingfield MJ, *et al.* (1998). Monophyly of the conifer species in the *Ceratocystis coerulescens* complex based on DNA sequence data. *Mycologia* **90**: 96–101.
- Yamaoka Y, Wingfield MJ, Ohsawa M, *et al.* (1998). Ophiostomatoid fungi associated with *Ips cembrae* in Japan and their pathogenicity of Japanese larch. *Mycoscience* **39**: 367–378.
- Yamaoka Y, Wingfield MJ, Takahashi I, *et al.* (1997). Ophiostomatoid fungi associated with the spruce bark beetle *Ips typographus* f. *japonicus* in Japan. *Mycological Research* **101**: 1215–1227.
- Yarwood CE (1981). The occurrence of *Chalara elegans*. *Mycologia* **73**: 524–530.