Redefining Ceratocystis and allied genera

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Abstract: The genus Ceratocystis was established in 1880 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 de

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

Taxonomic novelties: New genera:

- Davidsoniella
- Huntiella

New combinations:

- Chalaropsis ovoidea
- Ceratostomella nigra (Nag Raj & W.B. Kendr.)

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INTRODUCTION

Ceratocystis was established in 1890 to accommodate the 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 obvoid and that are either evenly or unevenly distributed around the spores (Fig. 3). The asexual states of most species in Ceratocystis are morphologically "chalaral"- or "thieviopsis"-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 chlamydospores (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. Wilted shoots of Acacia mearnsii 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. mearnsii 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. fimбриата. 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-infused 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, Withuhn et al. 1998, Harrington & Wingfield 1998). For example, perhaps the two best-known species names within Ceratocystis, C. fimбриата 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. fimбриата 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. adipoza 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. fimбриата complex are important and in some cases devastating plant pathogens (Kile 1993, Wingfield et al. 2013). These include C. albidus, 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, Ocaso-Morales et al. 2007), and C. manginecans that has devasted 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. 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. lmbriata*, CMW 15049), oblong (e.g. *C. paradoxa*, now *T. paradoxa*, CMW 36642) and obovoid (e.g. *C. lacticola*, now *E. lacticola*, CMW 20928). E–H. Simple tubular conidiophores commonly tapering to their apicies, 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. coerulescens (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. ethacetae), 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 Philalophopsis (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 bar-coding initiative (Schoch et al. 2012), as well as additional bar-coding genes from an ongoing project at CBS (Stielow et al. 2014) were used to design Microscales-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 (ACICGIGITICAGAYGTAAGCC) and Cer-MCM7R (TTRGCAACACCAAGRTGCACCCAT) 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 | Culture collection number(s) | Strain status | GenBank accession numbers |
|---------------|----------|---------|----------------|-----------------------------|-------------------|-----------------------------|---------------|--------------------------|
|               |          |         |                |                             |                   |                             |               |                          |
| **Ambrosiella beaveri** | Ambrosiella beaveri | USA | *Vitis rotundifolia* | D. Six; 2005 | – | CMW 26179; CBS 121753; DLS 1624 | ex-paratype | K495492 K495315 K495405 |
| **A. ferruginea** | A. ferruginea | Germany | *Fagus sylvatica* | G. Zimmerman; 1971 | – | CMW 25522; CBS 460.82 | not type | K495493 K495316 K495406 |
| **A. hartigii** | A. hartigii | Germany | *Acer sp.* | –; 1970 | – | CMW 25525; CBS 403.82 | not type | K495494 K495317 – |
| **A. xylebori** | A. xylebori | Ivory Coast | *Coffea canephora* | L. Brader; 1961 | – | CMW 25531; CBS 110.61 | ex-isotype | K495495 K495318 K495407 |
| **Ceratocystis acaciivora** | Ceratocystis acaciivora | Indonesia | *Acacia mangium* | M. Tarigan; 2005 | PREM 59884 | CMW 22563 | ex-holotype | K495496 K495319 K495408 |
| **C. adiposa** | C. adiposa | Japan | *Saccharum officinarum* | T. Miyake; 1934 | – | CMW 2573; CBS 136.34 | not type | K495497 K495320 K495409 |
| **C. albifundus** | C. albifundus | South Africa | *Acacia mellifica* | J. Roux; 1997 | – | CMW 4068; CBS 128992 | not type | K495498 K495321 K495410 |
| **C. atrox** | C. atrox | Australia | *Eucalyptus grandis* | M.J. Wingfield; 2005 | PREM 59012 | CMW 19385; CBS 120518 | ex-holotype | K495499 K495322 K495411 |
| **C. bhutanensis** | Huntella bhutanensis | Bhutan | *Picea spinulosa* | T. Kinits & D.B. Chhetri; 2001 | PREM 57804 | CMW 8217; CBS 114289 | ex-holotype | K495500 K495323 K495412 |
| **C. cacaofunesta** | C. cacaofunesta | Ecuador | *Theobromae cacao* | T.C. Harrington; 2000 | PREM 843731 | CMW 14803; CBS 115163; C 1695 | original collection | K495501 K495324 K495413 |
| **C. caryae** | C. caryae | USA | *Carya ovata* | J.A. Johnson; 2001 | – | CMW 14808; CBS 115168; C 1827 | original collection | K495502 K495325 K495414 |
| **C. cerberus** | Thieliavopsis cerberus | Cameroon | *Elaeis guineensis* | M. Mbenoun & J. Roux; 2010 | PREM 60770 | CMW 36668; CBS 130765 | ex-holotype | K495503 K495326 K495415 |
| **C. chineaucensis** | H. chineaucensis | China | *Eucalyptus grandis* & *E. urophylla* | M.J. Wingfield & S.F. Chen; 2006 | PREM 60735 | CMW 24658; CBS 127185 | ex-holotype | K495504 K495327 K495416 |
| **C. coerulescens** | Endocionidiphora coerulescens | Germany | *Picea abies* | T. Rohde; 1937 | – | CMW 26365; CBS 140.37; MUCL 9511; C 313; C 695 | not type | K495506 K495329 K495418 |
| **C. colombiana** | C. colombiana | Colombia | *Coffea arabica* | M. Marin; 2000 | PREM 59434 | CMW 5751; CBS 121792 | ex-holotype | K495507 K495330 K495419 |
| **C. corymbiicola** | C. corymbiicola | Australia | *Eucalyptus pilularis* | G. Kamgan Nkuekam; 2008 | PREM 60433 | CMW 29349; CBS 127216 | ex-paratype | K495508 K495331 K495420 |
| **C. curvata** | C. curvata | Ecuador | *Eucalyptus deglupta* | M.J. Wingfield; 2004 | PREM 60154 | CMW 22432 | ex-paratype | K495509 K495332 K495421 |
| **C. decipiens** | H. decipiens | South Africa | *Eucalyptus saligna* | G. Kamgan Nkuekam & J. Roux; 2008 | PREM 60560 | CMW 30855; CBS 129736 | ex-holotype | K495510 K495333 K495422 |
| **C. diversaconidia** | C. diversaconidia | Ecuador | *Terminalia ivorensis* | M.J. Wingfield; 2004 | PREM 60160 | CMW 22445; CBS 123013 | ex-holotype | K495511 K495334 K495423 |
| **C. douglasii** | E. douglasii | USA | *Pseudotsuga taxifolia* | R.W. Davidson; 1951 | BPI 595613 = FP 70703 | CMW 26367; CBS 556.97 | ex-holotype | K495512 K495335 K495424 |
| **C. ecuadoriana** | C. ecuadoriana | Ecuador | *Eucalyptus deglupta* | M.J. Wingfield; 2004 | PREM 60155 | CMW 22092; CBS 124020 | ex-holotype | K495513 K495336 K495425 |
| **C. ethacetica** | T. ethacetica | Malaysia | *Ananas comosus* | A. Johnson; 1952 | PREM 60961 | CMW 37775; IMI 50560; MUCL 2170 | ex-epitype | K495514 K495337 K495426 |

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| Previous name | New name | Country | Host/substrate | Collector; collection year | Herbarium Specimen | Culture collection number(s) | Strain status | GenBank accession numbers |
|---------------|----------|---------|----------------|---------------------------|-------------------|----------------------------|---------------|-------------------------|
| C. eucalypti  | Davidsoniella eucalypti | Australia | Eucalyptus sieberi | M.J. Dudzinski; 1989 | DAR 70205 | CMW 3254; C 639 | ex-holotype | KM495515 KM495338 KM495427 |
| C. eucalyptica | C. eucalyptica | South Africa | Eucalyptus sp. | M. van Wyk & J. Roux; 2002 | PREM 60168 | CMW 11536; CBS 124016 | ex-holotype | KM495516 KM495339 KM495428 |
| C. fagacearum | C. fagacearum | USA | Quercus rubra | S. Seegmuller; 1991 | – | CMW 2656; C463 | not type | KM495518 KM495341 KM495430 |
| C. ficicola | C. ficicola | Japan | Ficus carica | Y. Kajitani; 1990 | NIAES 20600 | CMW 38543; MAFF 625119 | ex-holotype | KM495519 KM495342 KM495431 |
| C. fimbriata | C. fimbriata | USA | Ipomoea batatas | C.F. Andrus; 1937 | – | CMW 15049; CBS 141.37 | not type | KM495520 KM495343 KM495432 |
| C. fimbriotomima | C. fimbriotomima | Venezuela | Eucalyptus hybrid | M.J. Wingfield; 2006 | PREM 59439 | CMW 21474; CBS 121786 | ex-holotype | KM495521 KM495344 KM495433 |
| C. fujianensis | E. fujianensis | Japan | Larix kaempferi | M.J. Wingfield & Y. Yamaoka; 1997 | PREM 57513 | CMW 1905; CBS 100208; JCM 9810 | ex-holotype | KM495522 KM495345 KM495434 |
| C. haringtonii | C. haringtonii | Netherlands | Populus hybrid | J. Gremmen; 1978 | – | CMW 14789; CBS 119.78; C 995 | original collection | KM495523 KM495346 KM495435 |
| C. inquinans | H. inquinans | Indonesia | Acacia mangium | M. Tarigan; 2005 | PREM 59866 | CMW 21106; CBS 124388 | ex-holotype | KM495524 KM495347 KM495436 |
| C. laricicola | E. laricicola | UK | Larix decidua | D. Redfern; 1983 | – | CMW 20928; CBS 100207; C 181; Redfern 56-10 | ex-paratyp  | KM495525 KM495348 KM495437 |
| C. larium | C. larium | Indonesia | Styax benzoin | M.J. Wingfield; 2007 | PREM 60193 | CMW 25434; CBS 122512 | ex-holotype | KM495526 KM495349 | – |
| C. major | C. adiposa | Netherlands | Air | F.H. van Beyma; 1934 | – | CMW 3189; CBS 138.34; ATCC 11932; MUCL 9518 | ex-holotype | KM495527 KM495350 KM495438 |
| C. mangicola | C. mangicola | Brazil | Mangifera indica | C.J. Rosetto; 2008 | PREM 60185 | CMW 28908; CBS 127210 | ex-paratyp  | KM495528 KM495351 KM495439 |
| C. manginecans | C. manginecans | Oman | Prosopis cineraria | A. Al Adawi; 2005 | – | CMW 17570; CBS 138185 | not type | KM495529 KM495352 KM495440 |
| C. mangivora | C. mangivora | Brazil | Mangifera indica | C.J. Rosetto; 2001 | PREM 60570 | CMW 27305; CBS 128702 | ex-holotype | KM495530 KM495353 KM495441 |
| C. microbasis | H. microbasis | Indonesia | Acacia mangium | M. Tarigan; 2005 | PREM 59872 | CMW 2117 | ex-holotype | KM495531 KM495354 KM495442 |
| C. moniliformis | H. moniliformis | South Africa | Eucalyptus grandis | M. van Wyk; 2002 | – | CMW 10134; CBS 118127 | not type | KM495532 KM495355 KM495443 |
| C. monilformopais | H. monilformopais | Australia | Eucalyptus obliqua | Z.Q. Yuan; 2001 | DAR 74608 | CMW 9986; CBS 109441 | ex-holotype | KM495533 KM495356 KM495444 |
| C. musarum | T. musarum | New Zealand | Musa sp. | T.W. Canter-Visscher; 2006 | PREM 60962 | CMW 1546; C 907 | ex-epitype | KM495534 KM495357 KM495445 |
| C. neglecta | C. neglecta | Colombia | Eucalyptus grandis | C. Rodas & J. Roux; 2004 | PREM 59616 | CMW 17808; CBS 121789 | ex-holotype | KM495535 KM495358 KM495446 |
| C. oblonga | H. oblonga | South Africa | Acacia mearnsii | R.N. Heath; 2006 | PREM 59792 | CMW 23803; CBS 122291 | ex-holotype | KM495536 KM495359 KM495447 |
| C. obpyriformis | C. obpyriformis | South Africa | Acacia mearnsii | R.N. Heath; 2006 | PREM 59796 | CMW 23808; CBS 122511 | ex-holotype | KM495537 KM495360 KM495448 |
| C. omanensis | H. omanensis | Oman | Mangifera indica | A. Al Adawi & M. Deadman; 2003 | – | CMW 11056; CBS 118113 | original collection | KM495538 KM495361 KM495449 |
| C. papillata | C. papillata | Colombia | Citrus x Tangelo hybrid | B. Castro; 2001 | PREM 59438 | CMW 8856; CBS 121793 | ex-holotype | KM495539 KM495362 KM495450 |

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

(continued on next page)
| Previous name   | New name     | Country    | Host/substrate                      | Collector; collection year | Herbarium Specimen | Culture collection number(s) | Strain status | GenBank accession numbers |
|----------------|--------------|------------|-------------------------------------|-----------------------------|-------------------|----------------------------|---------------|--------------------------|
|                |              |            |                                     |                             |                   | 60S LSU MCM7               |              |
| C. zambeziensis| C. zambeziensis | South Africa | Acacia nigrescens                  | M. Mbenoun & J. Roux; 2010  | PREM 60826        | CMW 35963; CBS 131282      | ex-paratype   | KM495563 KM495386 KM495473 |
| Chalaropsis sp. 1 | Chalaropsis sp. 1 | Belgium | Populus sp.                          | R. Veldeman; 1975           | –                 | CMW 22737; CBS 180.75      | not type      | KM495580 KM495403 KM495490 |
| Chalaropsis sp. 1 | Chalaropsis sp. 1 | USA       | Ulmus sp.                           | R.W. Davidson; 1939         | –                 | CMW 22738; CBS 130.39; C 1378; MUCL 9540; RWD E-1 | not type      | KM495581 KM495404 KM495491 |
| Graphium fabiforme | Graphium fabiforme | Madagascar | Dead Adansonia rubrostipa          | J. Roux & M.J. Wingfield; 2007 | PREM 60310        | CMW 30626; CBS 124921      | ex-holotype   | KM495564 KM495387 KM495474 |
| G. fimbrisporum | G. fimbrisporum | France     | Ips typographus gallery, in stump of Picea abies | M. Morelet; 1992            | –                 | CMW 5605; CBS 870.95; MPFN 281-8 | ex-holotype   | KM495565 KM495388 KM495475 |
| G. laricis     | G. laricis   | Austria    | Symmata occurring in galleries of the bark beetle Ips cembrae | T. Kirisits & P. Baier; 1995 | DAOM 229757       | CMW 5601; CBS 116194; DAOM 229757; IFFF ICL/MEA/13 | ex-holotype   | KM495566 KM495389 KM495476 |
| G. pseudomicricum | G. pseudomicricum | South Africa | Pinus sp.                         | M.J. Wingfield; 1984        | PREM 51539        | CMW 503                    | ex-holotype   | KM495567 KM495390 KM495477 |
| H. clamydofomis nom. prov. | H. clamydofomis nom. prov. | Cameroon | Theobromae cacao                  | M. Mbenoun & J. Roux; 2009 | PREM 60837        | CMW 36932; CBS 131674      | ex-holotype   | KM495505 KM495328 KM495417 |
| H. pycanthi nom. prov. | H. pycanthi nom. prov. | Cameroon | Theobromae cacao                  | M. Mbenoun; 2009            | PREM 60835        | CMW 36916; CBS 131672      | ex-holotype   | KM495547 KM495370 KM495458 |
| Knodvaviensia capensis | Knodvaviensia capensis | South Africa | Protea longifolia                | M.J. Wingfield; 1984        | –                 | CMW 997; CBS 120015        | not type      | KM495568 KM495391 KM495478 |
| K. cecropiae | K. cecropiae | Costa Rica | Cecropia angustifolia              | L. Kirkendall & J. Hulcr; 2005 | PRM 858080       | CMW 22991; CCF 3565        | ex-holotype   | KM495569 KM495392 KM495479 |
| K. proteae     | K. proteae   | South Africa | Protea repens flower infested with insects | L.J. Strauss; 1985          | PREM 48924        | CMW 738; CBS 486.88        | ex-holotype   | KM495570 KM495393 KM495480 |
| K. serotectus | K. serotectus | South Africa | Grow on insect (Cossonus sp.) found in Euphorbia ingens | J.A. van der Linde & J. Roux; 2009 | PREM 60566        | CMW 36767; CBS 129738      | ex-holotype   | KM495571 KM495394 KM495481 |
| K. ubusi | K. ubusi | South Africa | Insect tunnels in Euphorbia tetragona | J. Roux; 2010               | PREM 60568        | CMW 36769; CBS 129742      | ex-holotype   | KM495572 KM495395 KM495482 |
| Thielaviopsis australis | D. australis | Australia | Nothofagus cunninghamii          | M. Hall; 2001               | –                 | CMW 2333                   | not type      | KM495573 KM495396 KM495483 |
| T. basicola | T. basicola | Netherlands | Lathyrus odoratus                | G.A. van Arkel; –           | –                 | CMW 7068; CBS 413.52       | not type      | KM495574 KM495397 KM495484 |
| T. ceramica | T. ceramica | Malawi     | Eucalyptus grandis                | R.N. Heath & J. Roux; 2004  | PREM 59808        | CMW 15245; CBS 122299; CMW 15251 | ex-holotype   | KM495575 KM495398 KM495485 |
| T. eurici | T. eurici | Brazil | Air                               | E.A.F. da Matta; 1956       | URM 640          | CMW 28537; CBS 893.70; MUCL 1807; UAMH 1382 | ex-holotype   | KM495517 KM495340 KM495429 |
| T. neocaledoniae | D. neocaledoniae | New Caledonia | Coffea robusta                    | R. Dadant; 1948            | –                 | CMW 3270; CBS 149.83; C 694 | ex-holotype   | KM495576 KM495399 KM495486 |
| Previous name | New name | Country | Host/substrate | Collector; Herbarium | Culture collection number(s)1 | Strain status | GenBank accession numbers | LSU | 60S | MCM7 |
|---------------|----------|---------|----------------|----------------------|-------------------------------|--------------|------------------------|------|-----|------|
|               | T. ovoidea | Germany | Quercus petraea | H. Kleinhempel; 1987 | CMW 22733; CBS 1375; MUCL 6236 | no type | KM495577 |                 |                 | 50484 |
|               | T. ovoidea | Germany | Lupinus albus | R. Ciferri; 1937 | CMW 22736; CBS 148.37; MUCL 6238 | no type | KM495579 |                 |                 | 50486 |

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 Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CCM: Culture Collection of Microorganisms, Department of Plant Protection, Faculty of Agriculture, Charles University, Prague, Czech Republic; CMW: Culture collection of Mycology, University of Wisconsin-Madison, U.S.A.; 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 (IFFF), University of Natural Resources and Applied Life Sciences, Vienna (BOKU), Vienna, Austria; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, United Kingdom; JCM: Japan Collection of Microorganism, 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; MUC: Collection of Mycology, University of British Columbia, Vancouver, Canada; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium; NIES: National Institute of Environmental Research Science, Tokyo, Japan; NRM: Culture collection at the Natural Resources Institute, University of Greenwich, Medway, Kent, UK; NRC: Culture collection of the National Research Council of Canada, Ottawa, Canada; NSWC: Culture collection of the Ministry of Agriculture and Forestry, Japan; NIG: Natural Institute of Genetics, Ibaraki, Japan; PRM: Corda Herbarium, Prague, Czech Republic; R. W. Davidson, Department of Forest and Wood Sciences, Colorado State University, Fort Collins, Colorado, U.S.A.; and University of Panama, Panama, Republic of Panama; 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.

Phylogenetic analyses

Sequences from different gene regions were aligned using an online version of MAFFT v. 7 (Katoh & 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 ≥95%. Bootstrap support values ≥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 ≥95%. Bootstrap support values ≥70% are indicated at nodes as MP/ML. * = no bootstrap support or bootstrap support values <70%.

Ceratocystis sensu stricto

Ceratocystis

Endoconidiophora

Davidsoniella

Thielaviopsis

Huntiella

Ambrosiella

Knox Daviesia

Graphium

Redefining Ceratocystis and Allied Genera

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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 ≥95%. Bootstrap support values ≥70% are indicated at nodes as MP/ML. * = no bootstrap support or bootstrap support values <70%.

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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 ≥ 75%. Bootstrap support values ≥ 70% are indicated at nodes as MP/ML. * = no bootstrap support or bootstrap support values < 70%.

REDEFINING CERATOCYSTIS AND ALLIED GENERA

60S+LSU+MCM7

Ceratocystis sensu lato
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. fimбриa (type species of Ceratocystis) and 31 other species previously included in the C. fimбриa 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. neocaledonicae 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. eurcoi, C. musarum, C. radicicola and the recently described species, C. cerbersus. The sixth lineage was the second largest and included C. moniiformis 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.

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 aéuroconidia.

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 *Ceratocystis* | Current name | Basionym |
|------------------------|--------------|----------|
| C. abiicarpa R.W. Davidson | *Grosmannia* abiicarpa (R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf. | *Ceratocystis* abiicarpa R.W. Davidson |
| C. adjuncti R.W. Davidson | *Ophiostoma* adjuncti (R.W. Davidson) Harrington | *Ceratocystis* adjuncti R.W. Davidson |
| C. albidula (Math.-Käirik) J. Hunt | synonym of *Ophiostoma* stenoceras (Robak) Nannf. | *Ceratocystis* albidula Math.-Käirik |
| C. allantospora H.D. Griffin | *Ophiostoma* allantospora (Griffin) M. Villarreal | *Ceratocystis* allantospora H.D. Griffin |
| C. ambrosia Bakshi | *Ophiostoma* ambrosium (Bakshi) Hausner, J. Reid & Klassen | *Ceratocystis* ambrosia Bakshi |
| C. angusticollis Wright & H.D. Griffin | *Ophiostoma* angusticollis (Wright & Griffin) M. Villarreal | *Ceratocystis* angusticollis Wright & H.D. Griffin |
| C. araucariae Butin | *Ophiostoma* araucariae (Butin) de Hoog & Scheffer | *Ceratocystis* araucariae Butin |
| C. arborea Olchow. & J. Reid | *Ophiostoma* arborea (Olchow. & J. Reid) Yamaoka & M.J. Wingf. | *Ceratocystis* arborea Olchow. & J. Reid |
| C. aurea (R.C. Rob. & R.W. Davidson) H.P. Upadhyay | *Grosmannia* aurea (R.C. Rob. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf. | *Euphöium* aureum R.C. Rob. & R.W. Davidson |
| C. bacillospora Butin & G. Zimm. | *Ophiostoma* bacillospora (Butin & G. Zimm.) de Hoog & Scheffer | *Ceratocystis* bacillospora Butin & G. Zimm. |
| C. bicolor (R.W. Davidson & Wells) R.W. Davidson | *Ophiostoma* bicolor R.W. Davidson & D.E. Wells | *Ophiostoma* bicolor R.W. Davidson & D.E. Wells |
| C. brunnea R.W. Davidson | *Ophiostoma* brunneum (R.W. Davidson) Hausner & J. Reid | *Ceratocystis* brunnea R.W. Davidson |
| C. brunneo-ciliata (Math.-Käirik) J. Hunt | *Ophiostoma* brunneo-ciliatum Math.-Käirik | *Ceratocystis* brunneo-ciliatum Math.-Käirik |
| C. bruneocrinita E.F. Wright & Cain | *Graphilbum* bruneocrinatum (E.F. Wright & Cain) Z.W. de Beer & M.J. Wingf. | *Ceratocystis* bruneocrinita E.F. Wright & Cain |
| C. cainii Olchow. & J. Reid | *Grosmannia* cainii (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf. | *Ceratocystis* cainii Olchow. & J. Reid |
| C. californiae DeVay, R.W. Davidson & Moller | *Ophiostoma* californiae (DeVay, R.W. Davidson & Moller) Hausner, J. Reid & Klassen | *Ceratocystis* californiae DeVay, R.W. Davidson & Moller |
| C. cana (Münch) Moreau | *Ophiostoma* canum (Münch) Syd. | *Ceratostomella* cana Münch |
| C. capitata H.D. Griffin | synonym of *Ophiostoma* tenerum (R.W. Davidson) M. Villarreal | *Ceratostomella* capitata H.D. Griffin |
| C. castaneae (Vanin & Solovjev) C. Moreau | *Ophiostoma* castaneae (Vanin & Solovjev) Nannf. | *Ceratostomella* castaneae Vanin & Solovjev |
| C. catoniana (Goid.) C. Moreau | *Ophiostoma* catoniana (Goid.) Goid. | *Ceratostomella* catoniana Goid. |
| C. clavata (Math.) Hunt | *Ophiostoma* clavatum Math. | *Ophiostoma* clavatum Math. |
| C. clavigera (R.C. Rob. & R.W. Davidson) H.P. Upadhyay | *Grosmannia* clavigera (R.C. Rob. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf. | *Euphöium* clavigerum R.C. Rob. & R.W. Davidson |
| C. columnaris Olchow. & J. Reid | *Ophiostoma* columnare (Olchow. & J. Reid) Seifert & G. Okada | *Ceratocystis* columnaris Olchow. & J. Reid |
| C. concentrica Olchow. & J. Reid | *Ceratocystis* concentrica (Olchow. & J. Reid) H.P. Upadhyay | *Ceratocystis* concentrica Olchow. & J. Reid |
| C. coniciicollis Olchow. & J. Reid | *Ceratocystis* coniciicollis (Olchow. & J. Reid) H.P. Upadhyay | *Ceratocystis* coniciicollis Olchow. & J. Reid |
| C. coronata Olchow. & J. Reid | *Ophiostoma* coronatum (Olchow. & J. Reid) M. Villarreal | *Ceratocystis* coronata Olchow. & J. Reid |
| C. crassivaginata H.D. Griffin | *Grosmannia* crassivaginata (H.D. Griffin) Zipfel, Z.W. de Beer & M.J. Wingf. | *Ceratocystis* crassivaginata H.D. Griffin |
| C. crenulata Olchow. & J. Reid | *Ophiostoma* crenulatum (Olchow. & J. Reid) Hausner & J. Reid | *Ceratocystis* crenulata Olchow. & J. Reid |
| C. curvicolli Olchow. & J. Reid | *Graphilbum* curvicolle (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf. | *Ceratocystis* curvicolli Olchow. & J. Reid |
| C. davidsonii Olchow. & J. Reid | *Grosmannia* davidsonii (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf. | *Ceratocystis* davidsonii Olchow. & J. Reid |
| C. denticulata R.W. Davidson | *Ophiostoma* denticulatum (R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf. | *Ceratocystis* denticulata R.W. Davidson |
| C. distorta R.W. Davidson | *Ophiostoma* distortum (R.W. Davidson) de Hoog & Scheffer | *Ceratocystis* distorta R.W. Davidson |

(continued on next page)
| Name in Ceratocystis | Current name | Basionym |
|----------------------|--------------|----------|
| **C. dolomitina** H.D. Griffin | synonym of Ceratocystopsis minuta (Siemasko) H.P. Upadhyay & W.B. Kendr. | Ceratocystis dolomitina H.D. Griffin |
| **C. dryocoides** W.B. Kendr. & Molnar | Gromannia dryocoides (W.B. Kendr. & Molnar) Zipf, Z.W. de Beer & M.J. Wingf. | Ceratocystis dryocoides W.B. Kendr. & Molnar |
| **C. epigloea** Guerrero | Ophiostoma epigloea (Guerrero) de Hoog | Ceratocystis epigloea Guerrero |
| **C. eucastaneae** R.W. Davidson | synonym of Ophiostoma stenoceras (Robak) Nannf. | Ceratocystis eucastaneae R.W. Davidson |
| **C. eurhophodes** E.F. Wright & Cain | Gromannia eurhophodes (E.F. Wright & Cain) Zipf, Z.W. de Beer & M.J. Wingf. | Ceratocystis eurhophodes E.F. Wright & Cain |
| **C. fagi** (W. Loos) C. Moreau | synonym of Ophiostoma quercus (Georgev.) Nannf. | Ceratostomella fagi W. Loos |
| **C. falcata** E.F. Wright & Cain | Convesica falcata (E.F. Wright & Cain) C.D. Viljoen, M.J. Wingf. & K. Jacobs | Ceratocystis falcata E.F. Wright & Cain |
| **C. fasciata** | Ophiostoma fasciatum (Olichow. & J. Reid) Hausner, J. Reid & Klassen | Ceratocystis fasciata Olichow. & J. Reid |
| **C. fimbriata** (Marchal) H.P. Upadhyay | Sphaeronaemella fimbriata Marchal | Sphaeronaemella fimbriata Marchal |
| **C. floccosa** (Math.) J. Hunt | Ophiostoma floccosum Math. | Ophiostoma floccosum Math. |
| **C. franke-grossmanniae** R.W. Davidson | Gromannia franke-grossmanniae (R.W. Davidson) Zipf, Z.W. de Beer & M.J. Wingf. | Ceratocystis franke-grossmanniae R.W. Davidson |
| **C. fraxinopennsylvania** T.E. Hinds | Togninia fraxinopennsylvania (T.E. Hinds) Hausner, Eijolfsson & J. Reid | Ceratocystis fraxinopennsylvania T.E. Hinds |
| **C. galeiformis** Bakshi | Gromannia galeiformis (B.K. Bakshi) Zipf, Z.W. de Beer & M.J. Wingf. | Ceratocystis galeiformis Bakshi |
| **C. gossypina** R.W. Davidson | Ophiostoma gossypinum (R.W. Davidson) J. Taylor | Ceratocystis gossypina R.W. Davidson |
| **C. gossypina** var. robusta R.W. Davidson | synonym of Ophiostoma stenoceras (Robak) Nannf. | Ceratocystis gossypina var. robusta R.W. Davidson |
| **C. grandifoliae** R.W. Davidson | Gromannia grandifoliae (R.W. Davidson) Zipf, Z.W. de Beer & M.J. Wingf. | Ceratocystis grandifoliae R.W. Davidson |
| **C. helvellae** (P. Karst.) H.P. Upadhyay | Sphaeronaemella helvellae (P. Karst.) P. Karst. | Sphaeronaemella helvellae P. Karst. |
| **C. horanzskyi** Töth | Sphaeronaemella horanzskyi (Töth) Töth | Ceratocystis horanzskyi Töth |
| **C. huntii** R.C. Rob. | Gromannia huntii (R.C. Rob.) Zipf, Z.W. de Beer & M.J. Wingf. | Ceratocystis huntii R.C. Rob. |
| **C. hyalotheicum** R.W. Davidson | Ophiostoma hyalotheicum (R.W. Davidson) Hausner, J. Reid & Klassen | Ceratocystis hyalotheicum R.W. Davidson |
| **C. introcitrina** Olichow. & J. Reid | Ophiostoma introcitrinum (Olichow. & J. Reid) Hausner, J. Reid & Klassen | Ceratocystis introcitrina Olichow. & J. Reid |
| **C. Ips** (Rumbold) C. Moreau | Ophiostoma Ips (Rumbold) Nannf. | Ceratostomella Ips Rumbold |
| **C. leptographioides** (R.W. Davidson) J. Hunt | Gromannia leptographioides (R.W. Davidson) Zipf, Z.W. de Beer & M.J. Wingf. | Ceratostomella leptographioides R.W. Davidson |
| **C. leucocarpa** R.W. Davidson | Ophiostoma leucocarpum (R.W. Davidson) Z.W. de Beer & M.J. Wingf. | Ceratocystis leucocarpa R.W. Davidson |
| **C. longirostellata** Bakshi | Ophiostoma longirostellata (Bakshi) Arx & E. Müll. | Ceratocystis longirostellata Bakshi |
| **C. longispora** Olichow. & J. Reid | Ceratocystopsis longispora (Olichow. & J. Reid) H.P. Upadhayay | Ceratocystis longispora Olichow. & J. Reid |
| **C. macrospora** Aoshima [nom. inval., Art. 29.1, 36.1] | synonym of Gromannia laricis (K. van der Westh., Yamaoka & M.J. Wingf.) Zipf, Z.W. de Beer & M.J. Wingf. | Ceratocystis macrospora Aoshima [nom. inval., Art. 29.1, 36.1] |
| **C. megalobrunnea** R.W. Davidson & Toole | Ophiostoma megalobrunneum (R.W. Davidson & Toole) de Hoog & Schelle | Ceratocystis megalobrunnea R.W. Davidson & Toole |
| **C. microspora** (Arx) R.W. Davidson | Ophiostoma microsporum Arx | Ophiostoma microsporum Arx |
| **C. minima** Olichow. & J. Reid | Ceratocystis minima (Olichow. & J. Reid) H.P. Upadhayay | Ceratocystis minima Olichow. & J. Reid |
| **C. minor** (Hedgc.) J. Hunt | Ophiostoma minor (Hedgc.) Syd. | Ceratostomella minor Hedgc. |
| **C. minuta** (Siemasko) J. Hunt | Ceratocystis minuta (Siemasko) H.P. Upadhayay & W.B. Kendr. | Ophiostoma minuta Siemasko |
| **C. minuta-bicolor** R.W. Davidson | Ceratocystis minuta-bicolor (R.W. Davidson) H.P. Upadhayay & W.B. Kendr. | Ceratocystis minuta-bicolor R.W. Davidson |
| **C. montia** (Rumbold) J. Hunt | Ophiostoma montium (Rumbold) Arx | Ceratostomella montium Rumbold |

(continued on next page)
| Name in *Ceratocystis* | Current name | Basionym |
|------------------------|--------------|----------|
| C. *multiannulata* (Hedgc. & R.W. Davidson) J. Hunt | Ophistomata multiannulatum (Hedgc. & R.W. Davidson) Hendrix | Ceratostomella multiannulata Hedgc. & R.W. Davidson |
| C. *narcissii* (Limber) J. Hunt | Ophistomata narcissii Limber | Ophistomata narcissii Limber |
| C. *nigra* R.W. Davidson | Graphilbium nigrum (R.W. Davidson), Z.W. de Beer & M.J. Wingf. | Ceratostomella nigra R.W. Davidson |
| C. *nigrocarpa* R.W. Davidson | Ophistomata nigricarpum (R.W. Davidson) de Hoog | Ceratostomella nigrocarpa R.W. Davidson |
| C. *nothofagi* Butin | Ophiostoma nothofagi (Butin) Rulamort | Ceratostomella nothofagi Butin |
| C. *novae-zelandiae* Hutchison & J. Reid | synonym of Ophiostoma pluanniulatum (Hedgc.) Syd. | Ceratostomella novae-zelandiae Hutchison & J. Reid |
| C. *obscura* (R.W. Davidson) J. Hunt | Leptographium obscurum (R.W. Davidson) Z.W. de Beer & M.J. Wingf. | Ceratostomella obscura R.W. Davidson |
| C. *ochracea* H.D. Griffin | Ceratocystopsis ochracea (H.D. Griffin) H.P. Upadhyay | Ceratostomella ochracea H.D. Griffin |
| C. *olivaceapini* R.W. Davidson | Grosmannia olivaceapini (R.W. Davidson) Z.W. de Beer, Linnakoski & M.J. Wingf. | Ceratostomella olivaceapini R.W. Davidson |
| C. *ossiformis* Olchow. & J. Reid | synonym of Ophiostoma columnare (Olchow. & J. Reid) Seifert & G. Okada | Ceratostomella ossiformis Olchow. & J. Reid |
| C. *pallida* H.D. Griffin | synonym of Ceratostomopsis minuta-bicolor (R.W. Davidson) H.P. Upadhyay & W.B. Kendr. | Ceratostomella pallida H.D. Griffin |
| C. *pallido brunnea* Olchow. & J. Reid | Ceratocystopsis pallidobrunnea (Olchow. & J. Reid) H.P. Upadhyay | Ceratostomella pallidobrunnea Olchow. & J. Reid |
| C. *parva* Olchow. & J. Reid | Ceratocystopsis parva (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf. | Ceratostomella parva Olchow. & J. Reid |
| C. *penicillata* (Grosmann) C. Moreau | Grosmannia penicillata (Grosmann) Goed. | Ceratostomella penicillata Grosmann |
| C. *perfecta* R.W. Davidson | Ophiostoma perfectum (R.W. Davidson) de Hoog | Ceratostomella perfecta R.W. Davidson |
| C. *perпарvispora* J. Hunt | synonym of Ophiostoma microsporum Arx | Ceratostomella parparvispora J. Hunt |
| C. *piceae* (Münch) Bakshi | Ophiostoma piceae (Münch) Syd. | Ceratostomella piceae Münch |
| C. *piceiperda* (Rumbold) C. Moreau | Grosmannia piceiperda (Rumbold) Goed. | Ceratostomella piceiperda Rumbold |
| C. *pilifera* (Fr.) C. Moreau | Ophiostoma piliferum (Fr. : Fr.) Syd. | Sphaeria pilifera Fr. |
| C. *pini* (Münch) C. Moreau | synonym of Ophiostoma minus (Hedgc.) Syd. | Ceratostomella pini Münch |
| C. *pluanniulata* (Hedgc.) C. Moreau | Ophiostoma pluanniulatum (Hedgc.) Syd. | Ceratostomella pluanniulata Hedgc. |
| C. *polygrapha* Aoshima [nom. inval., Art. 29.1, 36.1] | synonym of Grosmannia aoshimae (Ohtaka, Masuya & Yamaoka) Masuya & Yamaoka | Ceratocystis polygrapha Aoshima [nom. inval., Art. 29.1, 36.1] |
| C. *ponderosae* T.E. Hinds & R.W. Davidson | synonym of Ophiostoma stenoceras (Robak) Nannf. | Ceratocystis ponderosae T.E. Hinds & R.W. Davidson |
| C. *populicola* Olchow. & J. Reid | Ophiostoma populicola (Olchow. & J. Reid) Z.W. de Beer, Seifert, M.J. Wingf. | Ceratocystis populicola Olchow. & J. Reid |
| C. *populina* T.E. Hinds & R.W. Davidson | Ophiostoma populinaum (T.E. Hinds & R.W. Davidson) de Hoog & Scheffer | Ceratocystis populina T.E. Hinds & R.W. Davidson |
| C. *pulcrofera* Kowalski Butin | Ophiostoma pulcrofera (Kowalski & Butin) Rulamort | Ceratocystis pulcrofera Kowalski & Butin |
| C. *pseudoeurophioides* Olchow. & J. Reid | Grosmannia pseudoeurophioides (Olchow. & J. Reid) Zipfel, Z.W. de Beer & M.J. Wingf. | Ceratocystis pseudoeurophioides Olchow. & J. Reid |
| C. *pseudominor* Olchow. & J. Reid | Ophiostoma pseudominor (Olchow. & J. Reid) Hausner, J. Reid & Klassen | Ceratocystis pseudominor Olchow. & J. Reid |
| C. *pseudonigra* Olchow. & J. Reid | Ophiostoma pseudonigra (Olchow. & J. Reid) Hausner, J. Reid & Klassen | Ceratocystis pseudonigra Olchow. & J. Reid |
| C. *pseudotsugae* (Rumbold) C. Moreau | Ophiostoma pseudotsugae (Rumbold) Arx | Ceratostomella pseudotsugae Rumbold |
| C. *quereri* (Georgiev.) C. Moreau | Ophiostoma querceri (Georgiev.) Nannf. | Ceratostomella querceri Georgiev. |
| C. *retusi* R.W. Davidson & T.E. Hinds | Ophiostoma retusi (R.W. Davidson & T.E. Hinds) Hausner, J. Reid & Klassen | Ceratocystis retusi R.W. Davidson & T.E. Hinds |
| C. *roboris* (Georgescu & Teodoru) Pott. | synonym of Ophiostoma quercus (Georgiev.) Nannf. | Ophiostoma roboris Georgescu & Teodoru |
| C. *robusta* (R.C. Rob. & R.W. Davidson) H.P. Upadhyay | Grosmannia robusta (R.C. Rob. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf. | Ceratocystis robustum R.C. Rob. & R.W. Davidson |
| C. *rostrocoronata* R.W. Davidson & Eslin | Ophiostoma rostrocoronatum (R.W. Davidson & Eslin) de Hoog & Scheffer | Ceratocystis rostrocoronatum R.W. Davidson & Eslin |

(continued on next page)
Table 2. (Continued).

| Name in Ceratocystis | Current name | Basionym |
|----------------------|--------------|----------|
| C. rostrocylindrica (R.W. Davidson) J. Hunt | Leptographium rostrocylindricum (R.W. Davidson) Z.W. de Beers & M.J. Wingf. | Ceratostomella rostrocylindrica R.W. Davidson |
| C. sagsatospora E.F. Wright & Cain | Grosmaniella sagsatospora (E.F. Wright & Cain) Zipfel, Z.W. de Beers & M.J. Wingf. | Ceratostomella sagatospora E.F. Wright & Cain |
| C. serpens (Goid.) C. Moreau | Grosmaniella serpens Goid. | Grosmaniella serpens Goid. |
| C. shikotsuensis Aoshima [nom. inval., Art. 29.1, 36.1] | synonym of Grosmaniella euphoricideae (E.F. Wright & Cain) Zipfel, Z.W. de Beers & M.J. Wingf. | Ceratostomella shikotsuensis Aoshima [nom. inval., Art. 29.1, 36.1] |
| C. sparsa R.W. Davidson | Graphiotrema sparsa H.P. Upadhyay & W.B. Kendr. | Ceratostomella sparsa R.W. Davidson |
| C. spinifera Olchow. & J. Reid | synonym of Ophiostoma fasciatum (Olchow. & J. Reid) Hauser, J. Reid & Klassen | Ceratostomella spinifera Olchow. & J. Reid |
| C. spinulosa H.D. Griffin | Ceratostomella spinulosa (H.D. Griffin) H.P. Upadhyay | Ceratostomella spinulosa H.D. Griffin |
| C. stenoceras (Robak) C. Moreau | Ophiostoma stenoceras (Robak) Nannf. | Ceratostomella stenoceras Robak |
| C. tenella R.W. Davidson | Ophiostoma tenellum (R.W. Davidson) M. Villarreal | Ceratostomella tenellum R.W. Davidson |
| C. tetropii (Math.) J. Hunt | Ophiostoma tetropii Math. | Ceratostomella tetropii (Math.) J. Hunt |
| C. torticiliata Olchow. & J. Reid | Ophiostoma torticiliata (Olchow. & J. Reid) Seifert & G. Okaide | Ceratostomella torticiliata Olchow. & J. Reid |
| C. torulosa Butin & G. Zimm. | Ophiostoma torulosum (Butin & G. Zimm.) Hauser, J. Reid & Klassen | Ceratostomella torulosum Butin & G. Zimm. |
| C. tremulo-aurea R.W. Davidson & T.E. Hinds | Ophiostoma tremulo-aureum (R.W. Davidson & T.E. Hinds) de Hoog & Schleifer | Ceratostomella tremulo-aureum R.W. Davidson & T.E. Hinds |
| C. triangulospora (Butin) H.P. Upadhyay | Ophiostoma triangulosporum Butin | Ceratostomella triangulosporum Butin |
| C. truncicola (R.W. Davidson) H.D. Griffin | Grosmaniella truncicola (R.W. Davidson) Z.W. de Beers & M.J. Wingf. | Ceratostomella truncicola R.W. Davidson |
| C. tubicollis Olchow. & J. Reid | Graphiotrema tubicollis (Olchow. & J. Reid) Z.W. de Beers & M.J. Wingf. | Ceratostomella tubicollis Olchow. & J. Reid |
| C. ulmi (Buisman) C. Moreau | Ophiostoma ulmi (Buisman) Nannf. | Ceratostomella ulmi Buisman |
| C. valachicum (Georgescu, Teodoru & Badea) Polt. | Ophiostoma valachicum Georgescu, Teodoru & Badea | Ceratostomella valachicum Georgescu, Teodoru & Badea |
| C. vesca R.W. Davidson | Grosmaniella vesca (R.W. Davidson) Zipfel, Z.W. de Beers & M.J. Wingf. | Ceratostomella vesca R.W. Davidson |
| C. wageneri Goheen & F.W. Cobb | Grosmaniella wageneri (Goheen & F.W. Cobb) Zipfel, Z.W. de Beers & M.J. Wingf. | Ceratostomella wageneri 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.

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. Ascii 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. Aleuroconidia 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 albidifundus 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.
2 Species that have thielaviopsis-like asexual states and probably belong to genera in the Ophiostomatales.

**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 *Ceratocystis* | Basionym | Probable ordinal, generic placement |
|------------------------|----------|-----------------------------------|
| *C. acenica* H.D. Griffin | *Ceratostomella acenica* H.D. Griffin | Ophiostomatales, *Ophiostoma* s.l. or *Leptographium* s.l. |
| *C. acoma* (V.V. Miller & Cernzow) C. Moreau | *Ceratostomella acoma* V.V. Miller & Cernzow | Ophiostomatales, *Ophiostoma* s. str. |
| *C. aequivaginata* Olchow. & J. Reid | *Ceratostomella aequivaginata* Olchow. & J. Reid | Ophiostomatales, *Leptographium* s.l. |
| *C. alba* DeVay, R.W. Davidson & W.J. Moller | *Ceratocystis alba* DeVay, R.W. Davidson & W.J. Moller | Peripheral to Ophiostomatales |
| *C. autographa* Bakshi | *Ceratocystis autographa* Bakshi | Sordariomycetidae, *incertae sedis* |
| *C. brevicollis* R.W. Davidson | *Ceratocystis brevicollis* R.W. Davidson | Ophiostomatales, *Ophiostoma* s.l. or *Leptographium* s.l. |
| *C. buxi* (Borissov) C. Moreau | *Ceratostomella buxi* Borissov | Sordariomycetidae, *incertae sedis*, *Ceratostomella* |
| *C. comata* (V.V. Miller & Cernzow) C. Moreau | *Ceratostomella comata* V.V. Miller & Cernzow | Ophiostomatales, *Leptographium* s.l. |
| *C. deltoideospora* Olchow. & J. Reid | *Ceratostomella deltoideospora* Olchow. & J. Reid | Ophiostomatales, *Raffaelea* |
| *C. grandicarpa* Kowalski & Butin | *Ceratostomella grandicarpa* Kowalski & Butin | Ophiostomatales, genus uncertain |
| *C. imperfecta* (V.V. Miller & Cernzow) C. Moreau | *Ceratostomella imperfecta* V.V. Miller & Cernzow | Ophiostomatales, *Leptographium* s.l. |
| *C. magnifica* H.D. Griffin | *Ceratocystis magnifica* H.D. Griffin | Ophiostomatales, *Ophiostoma* s.l. |
| *C. merolimensis* (Georgiev.) C. Moreau | *Ceratostomella merolimensis* Georgiev. | Sordariomycetidae, *incertae sedis*, *Ceratostomella* |
| *C. microcarpa* (P. Karst.) C. Moreau | *Ceratostomella microcarpa* P. Karst. | Sordariomycetidae, *incertae sedis*, *Ceratostomella* |
| *C. seticollis* R.W. Davidson | *Ceratocystis seticollis* R.W. Davidson | Ophiostomatales, genus uncertain |
| *C. stenospora* H.D. Griffin | *Ceratocystis stenospora* H.D. Griffin | Ophiostomatales, *Ophiostoma* s.l. or *Leptographium* s.l. |
| *C. trinaciformis* (A.K. Parker) H.P. Upadhyay | *Euophium trinaciforme* A.K. Parker | Ophiostomatales, *Ophiostoma* s.l. or *Leptographium* s.l. |
| *C. validiviana* Butin | *Ceratostomella validiviana* Butin | Ophiostomatales, *Leptographium* s.l. |

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

**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.

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

**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 *Ceratocystis* | Basionym | Reason for invalidity |
|------------------------|----------|-----------------------|
| *C. antennaroidospora* Roldán | *Ceratocystis antennaroidospora* Roldán | Art. 40.1 |
| *C. asteroides* Roldán | *Ceratocystis asteroides* Roldán | Art. 40.1 |
| *C. chinensis* G.H. Zhao | *Ceratocystis chinensis* G.H. Zhao | Art. 40.1, 40.6 |
| *C. heveae* G.H. Zhao | *Ceratocystis heveae* G.H. Zhao | Art. 40.6 |
| *C. jezoensis* Aoshima | *Ceratocystis jezoensis* Aoshima | Art. 29.1 & 36.1 |
| *C. kubanica* (Sczerbin-Parfenenko) Potlajchuk | *Ophiostoma kubanica* Sczerbin-Parfenenko | Art. 36.1 |
| *C. minor* (Hedgc.) J. Hunt var. barrasi J.J. Taylor | *Ceratocystis minor* (Hedgc.) J. Hunt var. barrasi J.J. Taylor | Art. 40.1 |
| *C. podiciphikovi* Milko | *Ceratocystis podiciphikovi* Milko | Art. 40.1 |
| *Thielaviopsis walleniiiformis* Dominik & Ihnat. | *Thielaviopsis walleniiiformis* 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*. 

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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                  | Notes                                                                 |
|--------------------------|----------------------------------------------------------------------|
| Ceratocystis perneri      | Jaekel                                                                |
| Ceratocystis prosthiaikia| Rahman, Zamora & Geyer                                               |
| Ceratocystis spinosa      | Ubaghs                                                                |
| Ceratocystis vizcainoi    | Ubaghs                                                                |

Ceratocystis corymbiicola 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., Fungal Diversity 46: 122. 2011.

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 fimbriatum (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); Olchowiecki & Reid (1974: 1699, pl. XII, 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 Rostella 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 fimbiatominima 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 mbriatominima M. van Wyk & M.J. Wingf., IMA Fungus 3: 54. 2012.

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

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., Mycotaxon 117: 395. 2011.

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 zombamontana M. van Wyk & M.J. Wingf., Fungal Diversity 40: 112. 2010.

Notes: Kamgan & Jol. Roux, Antonie van Leeuwenhoek 101: 237. 2012.
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 & Caprelli 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 thulamelensis 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. Ascii 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 one-celled, elongate, narrow fusiform, attened ends, barrel-shaped, hyaline, borne in chains of varying length. Aleuroconidia 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.

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.

Note: Sexual state unknown.

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.

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 16: 212. 1952.

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

Notes: Hunt (1956), Ochowewski & Reid (1974), and Upadhayay (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. (1990) confirmed the separateness of the species.

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

≡ Ceratocystis Ellis & Halst. section Endoconidiophora (Münch) H.P. Upadhay pro parte, In: Upadhay, Monogr. Ceratocystis & Cerato-cystiopsis: 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 colletare. Conidiogenous cells phialidic, oblong cylindrical. Conidia unicellular, rectangular with two attachment points, hyaline, in chains. Aleuroconidia 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.

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); Upadhay (1981: 65, figs 191–196); Potlaczuk & 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. pini cola, 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:** Upadhay (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 fujien sis** (M.J. Wingf., Yamaoka & Marin) Z.W. de Beer, T.A. Duong & M.J. Wingf., **comb. nov.** MycoBank MB810313.

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

**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. fujienensis* based on differences in bark beetle associates, conifer hosts and molecular data.

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

Basionym: *Ceratocystis lariccola* 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:** The most distinctive features of this genus are the conical ascomatal necks, and the hat-shaped ascospores.

**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”).

**Huntiella** 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:** *Huntiella 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. **Aleuroconidia** not observed.

**Notes:** 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.

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

Basionym: *Thiealviosis ceramic*a R.N. Heath & Jol. Roux, Fungal Diversity 34: 60.

Note: Sexual state unknown.

**Huntiella chineaeensis** (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 chineaeensis* S.F. Chen, M. van Wyk, M.J. Wingf. & X.D. Zhou, Fungal Diversity 58: 274. 2013.

**Huntiella cryptoform**is (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 moniliform**is (Hedg.) Z.W. de Beer, T.A. Duong & M.J. Wingf. comb. nov. MycoBank MB810325.

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

≡ *Ophiostoma moniliforme* (Hedg.) Syd., *In Sydow & Sydow, Ann. Mycol.* 17: 43. 1919.
≡ *Endoconidiophora moniliformis* (Hedg.) R.W. Davidson, J. Agric. Res. 50: 800. 1935.
≡ *Ceratocystis moniliformis* (Hedg.) M. Moreau & Moreau, Rev. Mycol. (Paris) Suppl. Col. 17: 141. 1952. (nom. illegit., Art. 52.1).
≡ *Ceratocystis moniliformis* (Hedg.) 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 “Iunae”).
≡ *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. pycnathi 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* Roldán, 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); Upadhay (1981: 51, figs 109–115); Maekawa et al. (1987: 8–10, figs 7–18); Kowalski & Butn (1989: 238–241).

Notes: Four varieties were described invalidly for *C. moniliformis* by Luc (1952). Moreau & Moreau (1952) then reduced these two species, *C. wilsonii* and *C. variospora* (now considered a distinct species), to formae of *C. moniliformis*, and treated *R. coffeae* as a synonym (see notes above under *C. fimbiata*). Moreau & Moreau (1952) reduced *O. moniliforme* f. theobromae to synonymy with *C. moniliformis*, and Hunt (1956) did the same with *C. bunae* and *C. wilsonii*. Nag Raj & Kendrick (1975) and Upadhay (1981) added *C. filiformis* to the synonyms of *C. moniliformis*. The accuracy of all these synonyms 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. 1904. (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. Ostiolar hyphae divergent, hyaline. Asci dehiscent. Ascospores aseptate, ellipsoidal, hyaline with sheath. Conidiophores lageniform, solitary, occasionaly 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 distinctly digitate or stellate appendages on the ascomatal bases.

**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”).

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

= *Catenularia echinata* Wkkrer, 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. inv. by 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 paradoxa* (De Seynes) Narr., Svenska Skogsv.-Före. 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. 1962.

= *Stillbochalaria 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 (1961: 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: *Chalara punctulata* Hennebert, Antonie van Leeuwenhoek 33: 334. 1967.

Note: The synonymy between *T. punctulata* and *C. punctulata* is 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).
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. radicicola 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. radicicola, 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: Sphaeroma adiposum Butler, Mem. Dept. Agric. India, Bot. Ser. 1: 40. 1906.

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), Olchowekki & 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. S. 5: 461. 1850.

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.

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.

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 *Endoconiidiophora*), 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. imbricata*. 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 *Huntiella* (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. cacao funesta*, and *C. albifundus* (Wingfield et al. 1996, Engelbrecht & Harrington 2005). In others, distinction at the species level has been debated (Fouri 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 *Endoconiidiophora* 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. lari-icola*, *E. lariicus* 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., *Huntiella* 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 *Endoconiidiophora*, but for which material was not available, should be considered in future treatments of this genus.

*Davidiasoniella* 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 *Endoconiidiophora*. The remaining two species (*D. australis* and *D. neocaledoniae*) are known only by their asexual morphs, with the “chalarra- 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 *Davidiasoniella*, 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).

*Huntiella* 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 *Huntiella* of which 18 were included in the analyses. Two of these species are in the process of being described (Mbenoun unpubl. data). Species of *Huntiella* 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). *Huntiella* 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" conidigenous 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 recognized 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-recognized plant pathogens (Butler 1906, Yearwood 1981, Juzwik et al. 2009) and we recognize 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 recognize 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 single 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 assexual 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.

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